THE TRANSLOCATION OF METABOLITES IN NAVEL ORANGE

By

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The effects of GA on fruit set and distribution of metabolites in fruiting shoots of navel orange were studied when GA was applied as individual flower dips and as whole tree sprays. Individual flowers dipped in GA resulted in a large increase in fruit set when compared to the control, but GA sprays applied to entire trees were ineffective.

There was a stronger movement of ^{14}C-metabolites into ovaries and young fruits throughout the fruit-setting period from both current season and previous season leaves of the GA-dip treatment than for untreated trees or those sprayed with GA. In addition, the GA-spray treatment and the control had a period of reduced transport from old leaves to fruits, following anthesis, before new leaves began exporting significant quantities to fruits.

Dry wt of fruits from the GA-dip treatment and the control was much greater than fruit from the GA-spray treatment.

Fruits were the primary site of importation of metabolites from a median leaf on the shoot; however there was some basipetal movement, particularly just prior to expansion of the summer flush.

The strongest fruit-setting treatment maintained a greater movement of metabolites from the leaves into fruits than other treatments, substantiating the hypothesis that growth regulators promote fruit set by enhancing the movement of metabolites into fruits. The failure of whole tree sprays of GA to enhance fruit set of navel orange appears to be due to an inability of the fruit to attract metabolites in sufficient quantities to maintain fruit growth during the fruit setting period.

INTRODUCTION

The navel sweet orange group (Citrus sinensis (L.) Osbeck) consists of a large number of morphologically similar cultivars recognized by the presence of a small, rudimentary secondary fruit embedded in the apex of the fruit -- the navel. Navel cultivars are of world-wide significance because of their distinctive fine quality, crisp flesh texture and ease of peeling. Navel oranges are almost entirely seedless because they rarely produce any functional pollen or fertile ovules. Yields of navel oranges are characteristically lower than those of seedy cultivars and strongly parthenocarpic seedless types. Low yields are at times partially attributable to preharvest fruit drop due to insects and diseases damaging the navel end of the fruit, but most unfruitfulness results from fruit drop due to environmental stress (19). Much research has been conducted to improve yields. Cross-pollination has been ineffective because of the lack of fertile ovules (28). Girdling has sometimes been effective and is a common practice in certain areas (94). Results from girdling are, however, inconsistent. Attempts to increase yields with auxin sprays have met with very limited success (18). Large increases in yields have occurred when either navel orange flowers or fruit were dipped into solutions of gibberellic acid (GA) (55), when GA has been applied as a dust to stigmatic surfaces of flowers and when a solution of GA has been applied only to the leaves just back of the flowers (53), but it has been ineffective when sprayed on entire trees.

Crane (22) has suggested that growth regulators, such as GA, promote fruit set by establishing a high rate of metabolic activity in the ovary which results in a continuous flow of metabolites from other parts of the plant and thereby maintaining fruit growth and preventing abscission. Powell (85), reported a continuous movement of ^{14}C-labelled metabolites from leaves to young fruit of the seedy Calamondin (C. madurensis Lour.) when sexually fertilized but not when pollen was excluded. Applications of GA to the flowers also resulted in a strong movement of metabolites to the young fruit and excellent parthenocarpic fruiting, thereby bolstering the metabolite hypothesis. Cytokinins and auxins also have a strong polarizing effect on the movement of metabolites into treated tissues (44, 39, 34, 38). Thus, the role of growth regulators in fruit set and development appears to be related to the supply of leaf-metabolites to the young fruit. The purpose of this work, therefore, was to investigate the movement of leaf-metabolites in the 'Washington' navel orange following the application of GA both as flower dips and as whole-tree sprays in order to determine why GA-sprays are ineffective on this cultivar.

LITERATURE REVIEW

Fruit Set

Fruits develop from the ovaries of flowers but flower formation alone does not guarantee a crop. Seed-bearing plants normally require the sexual processes of pollination and fertilization to stimulate the ovary into enlarging and remaining on the tree. Ovaries in which no fertilization of ovules occurs generally drop soon after flowering. The remaining ovaries soon enlarge perceptibly and often change color. Some describe this somewhat indefinite development as fruit set (61), thereby relating fruit set to the drop resulting from the lack of fertilization. This definition leaves much to be desired because many young fruit drop during a period of a month or more after the drop due to lack of fertilization (32). This drop is more or less continuous but there is often a distinctly large drop in late spring or early summer, often called the June drop, that has been related to competition for water and nutrients (34). Fruit set is also used to describe the early fruit development period terminated by the last significant fruit drop (32). This definition is useful because fruit remaining after the June drop are unlikely to fall prior to maturity and fruit counts taken after the June drop are often closely related to yield at maturity.

A relatively large number of fruit cultivars, including those in the navel orange group, produce fruit parthenocarpically; i.e., without sexual

fertilization and therefore without seeds (34). Thus, fruit set should not be used to indicate the fruit remaining after the initial drop due to a lack of fertilization, because in the case of parthenocarpic fruiting, fertilization does not occur. The term fruit set in this paper refers to the fruit development period extending from flowering through the June drop.

Cultivar Selection

Navel oranges mutate frequently and this has resulted in a large number of navel cultivars, many of which are almost indistinguishable from the original 'Washington' (43). The high rate of mutation has led numerous researchers and growers to search for higher yields.

Shamel and co-workers in California conducted an extensive but largely unsuccessful search for higher yielding, better quality strains of navel oranges (88, 89, 90, 91, 92, 93, 97, 98, 99). Reports from Texas (68) and Australia (26) indicate that some selections appear to be superior to old-line cultivars but the problem of low yields persists. Gardner and Reece (31) in Florida evaluated 28 selections of navel oranges over a 4-year-period and reported several numbered selections to be higher yielding than any of the commonly planted old lines. Numerous Florida growers have introduced mutations such as 'Summerfield', 'Dream' and 'Glen' for which claims of better yields were made (43) but these claims appear unjustified. Thus, even though improvement of yield by cultivar selection remains a possibility and limited success has been attained (31, 79), navel cultivars in Florida still suffer from low yields.

Cultural Practices and Environment

Coit and Hodgson (19) made an extensive study of abnormal fruit drop of 'Washington' navel orange. They concluded that the majority of the fruit

abscission early in the season was due to problems involving water relations, "resulting from the asperity of the climatic complex to which the trees are subject." They surveyed 'Washington' navel groves in various climatic areas of California and found that those in the cooler more humid areas would consistently produce more fruit than those in desert areas. The authors also found that climatic conditions in the orchard could be modified by various cultural practices which either reduced soil temperatures or created more favorable moisture relations. They hypothesized that such practices could be used to make orchards in the desert regions as productive as those in the more climatically favored districts; however, this has not been demonstrated.

Many environmental factors such as hot dry winds, high temperatures, low humidity, low rainfall, increase the water deficit of navel orange trees and cause abscission of young fruit. Site selection based upon soil type, annual rainfall, mean temperature, relative humidity, and wind protection has been means suggested to provide a more compatible environment (19, 83).

Effects of rootstock on yield of citrus in general are well established but the nature of the influence has not been established. Krezdorn and Phillips (56) working with the 'Orlando' tangelo in Florida reported that several rootstocks supported high yields of seedless fruit, but trees on other rootstocks yielded poorly. Later work (10) demonstrated that rootstocks varied greatly in depth of rooting, suggesting that those penetrating large volumes of soil might reduce the physiological stress due to inadequate soil moisture during the fruit-setting period and thereby increase fruiting. The largest yields were those of trees on the deepest rooted stocks, but some of the shallowest rooted ones also produced excellent crops. Thus,

even though the reasons some rootstocks resulted in higher yields were not established, the research demonstrated that a rootstock can in certain cases bring about satisfactory fruiting of a weakly parthenocarpic citrus cultivar. There has been no comparable rootstock research with navel oranges in Florida because certain viruses that have been present in all navel orange budwood sources cause stunting of trees on certain rootstocks and this has resulted in the abandonment of rootstock trials. None of the rootstocks used commercially in Florida satisfactorily overcome the navel orange fruiting problem.

Cross Pollination

Self-unfruitfulness results when sexual fertilization is not accomplished and parthenocarpy is lacking. The 'Bruce' plum and several peach cultivars are pollen sterile and require cross pollination (59, 11). The most common cause, however, of self-unfruitfulness is the result of sexual self-incompatibility. Cross pollination is necessary for fruit production in many fruit crops such as almonds (12), sweet cherries (81), many cultivars of apples (12, 60) and some pears (82). Most citrus cultivars are self-fruitful. Many interspecific hybrids such as 'Orlando' (57), 'Minneola' (57), 'Robinson', 'Osceola', and 'Nova' (87) are self-incompatible, however, and not sufficiently parthenocarpic to produce adequate crops without cross pollination or some other stimulus to strengthen the parthenocarpy.

Absence of pollen in the flowers of navel oranges removes any possibility of self-pollination and Webber (118) demonstrated that only a slight increase in seediness was caused by cross pollination. Pomeroy and Aldrich (84) and El-Tomi (27) reported slightly improved fruit set in some years by cross-pollinating individual navel flowers. Pomeroy and Aldrich, however, did not observe increased yield of 'Washington' navel trees planted

adjacent to other citrus cultivars. Workers in South Africa (26) pollinated 'Washington' navel flowers with pollen from 20 different citrus cultivars. There was a wide range of responses in both fruit set and number of seed per fruit. For example, 'Valencia' sweet orange pollen and 'Morton' citrange pollen did not increase seed number or fruit set in 'Washington' navel when compared to the unpollinated control; however, 'Bath' sweet orange pollen, and pollen from several grapefruit and shaddock cultivars significantly increased both seed number and fruit set. More importantly, pollen of 'Hamlin' sweet orange was nearly as effective as the pollen from the grapefruit and shaddock cultivars, setting 22% of the 'Washington' flowers pollinated, compared to 3.5% set parthenocarpically. There was an average of only 0.2 seeds per fruit resulting from the 'Hamlin' pollen, whereas shaddock pollen produced fruit having an average of 8 seeds per fruit. Since seedlessness is an important attribute of navel oranges, a pollen source which increases fruit set but not seed number would make a very desirable pollinator.

Girdling

Girdling, a very old horticultural practice, has been used with varying degrees of success in increasing parthenocarpy of many fruit crops, including pears (71), grapes (112, 111), persimmon (42), cherry (72), apples (71), and citrus (3, 33, 51, 58, 80, 95). The physiological response of fruit set to girdling is not well understood (51, 73, 78), but it is known to cause an accumulation of carbohydrates (73, 78), growth regulators (102, 112) and other substances (78, 103, 104, 114) above the girdle.

It is a common practice to girdle navel orange trees to increase fruit set in California. Adverse effects on tree condition have not been observed when trees were girdled annually for extended periods of time,

but there have been both positive (86) and negative reports (96) with respect to reductions in yield of subsequent crops when girdling was discontinued.

Work in Florida (51) indicates that girdling is inconsistent in increasing fruit set of navel oranges. Best results have been obtained on young, vigorous trees, with less success being achieved on older ones.

Growth Regulators

Auxins. The significance of auxins in fruit setting has been recognized for almost 40 years (22). Auxins are present in pollen and is produced in the style and ovary during pollen tube growth and fertilization. The resultant stimulation in growth of the ovary is an established fact (110). Relatively few citrus cultivars, however, have been induced to set fruit parthenocarpically by auxin application.

Auxins are most effective on fruits with many ovules, such as eggplant, fig, grape, strawberry and tomato (107, 24). Auxins have been ineffective on stone fruits, such as peach, plum, and cherry (107). Other fruits such as apple, apricot, avocado and pear may be set by auxin application, but usually fail to grow to normal size (24).

Work in California on citrus has shown negative results with 2, 4-dichlorophenoxyacetic acid (2,4-D), napthaleneacetic acid (NAA), indoleacetic acid (IAA), indolebutyric acid (IBA), and many other auxins in attempts to enhance fruit set with these materials (17). In South Africa, however, 2,4-D has increased yield of navel oranges through an increase in both numbers of fruit and fruit size (17). The difference in the reaction of navel oranges to 2,4-D in South Africa and California was explained as possibly due to the vast differences in environmental conditions

Gibberellins. Many types of fruit such as fig, tomato, eggplant, and citrus that can be set with auxins can also be set with GA. In addition, fruit set of many species responds to GA treatment but not to auxins, (21, 23, 26, 107). For example, some success has been achieved in increasing fruit set of apples with GA (25, 61, 65, 133), even though auxins have been ineffective. Applications of GA to pears has increased parthenocarpic fruit development; however, the benefit was only realized on low bearing cultivars of trees damaged by frost at blossom time (102).

Bukovac and Nakagawa (7) demonstrated a considerable difference in specificity among gibberellins in research with 'Wealthy' apple. Unpollinated controls abscissed within 4 weeks but the growth rate of fruit treated with GA_4 and GA_7 was equal to the pollinated controls. GA_5, GA_6 and GA_8 showed little activity and responses to several other gibberellins were intermediate.

Application of GA to small 'Bearss' lime fruit, 'Eureka' lemon flowers and flowering branches of 'Washington' navel orange trees resulted in an increased number of parthenocarpic fruit (40). Iwasaki et al. (46) applied GA individually to flowers and young fruit of 'Washington' navel and improved retention of the fruit. 'Clementine' mandarin has responded favorably to fruit set treatments of GA (80, 101) and substantial increases in set of 'Orlando' tangelo and other mandarin hybrids have been obtained with spray applications of GA (53, 54, 55)

Substantial increases in yield resulted when individual navel orange flowers were dipped in solutions of GA, (55), or applied to young leaves just behind the fruit (53). Whole tree sprays, however, have given varied responses from no effect on fruiting or leaf abscission in Florida (53) to severe leaf drop and death of new vegetative and flower-producing shoots in California (41).

Cytokinins. Increased fruit set of grapes (114) has been obtained with 6-benzylamino purine (BA) and 6-benzylamino-9-(2-tetrahydropyranyl)-9H-purine (PBA). PBA was effective in inducing parthenocarpic fruiting in fig (23). Cytokinins are reportedly useful in increasing fruit set in muskmelon (48) and in some apple cultivars (119) although they have been generally less effective than GA. Kriedemann demonstrated the ability of cytokinins to increase the transport of photosynthetic assimilates into young 'Washington' navel fruit; however, no beneficial effects on fruit set of citrus have been reported(49).

Many interactions and synergisms of cytokinins with other growth regulators have been demonstrated; however, they generally are less effective in inducing fruit set than GA.

Fruit Growth

The main blooming period of citrus cultivars is in the spring. Most cultivars bloom at nearly the same time; however, the developmental period varies, depending on the cultivar and the climate, from 7 to 13 months (100).

Fruit Growth Stages

Fruit growth is a result of cell division and cell enlargement. Expansion of intercellular spaces also contributes to the growth of fruit, especially during the later stages. Cell division usually predominates during early stages of fruit growth followed by cell enlargement. There is often an overlapping of the 2 stages and cell division persists until maturity in some fruits such as avocado (110).

The growth curve of some fruits, such as citrus, apple, pear, tomato, cucumber and strawberry is sigmoid in shape. Fig, currant, grape, blueberry, and many stone fruits, including cherry, olive, apricot, peach and plum, are characterized by a double sigmoid curve. Growth of the ovary in the latter type occurs in 2 stages separated by an inactive period of growth. It is during this period in stone fruits, when the ovary growth ceases, that the embryo and endosperm develops and lignification of the endocarp occurs (110, 76, 22, 61).

Morphological development of relatively few citrus cultivars has been investigated. Bain (4) working with 'Valencia' sweet orange made the most complete investigation of the development of any citrus cultivar. Adigun (2) demonstrated the effect of GA, girdling, and cross pollination on the development of 'Orlando' tangelo fruit.

Bain divided the developmental period of 'Valencia' orange into 3 growth stages: Stage I begins at bloom and lasts about 9 weeks. It is designated as the period of cell division since the number of cells in all tissues of developing fruit except the inner cells of the central axis, increase to form the tissue of the mature fruit during this period. Increase in fruit size during Stage I is due mainly to growth of the peel.

Stage II lasts for approximately 29 weeks and is the period of maximum fruit growth, with morphological, anatomical, and physiological changes being very rapid during this period. There is marked expansion of tissues accompanied by cell enlargement and differentiation during Stage II. Cell division continues in the outer peel tissues throughout Stage II The pulp expands considerably, the juice sacs become larger and the juice content increases. Stage II is considered as the critical period for fruit growth.

Stage III is designated the maturation period and lasts approximately 28 weeks. Fruit continue to grow during Stage III but at a reduced rate compared to Stage II. Ripening occurs during this period accompanied by a change of peel color from yellow to orange.

Bouma (6) made a study of 'Washington' navel orange development in relation to cultural and fertilizer practices. He found that different cultural systems evaluated had little effect on fruit morphology but that nitrogen level had a pronounced effect on peel thickness during Stage II. He surmised that the stages of development were substantially shorter for 'Washington' than Bain (4) had found for 'Valencia' since the total growing period was 5-6 months shorter. Bouma found, however, that Stage I in 'Washington' lasted 11 weeks or 2 weeks longer than the same growth stage of 'Valencia'. Stages II and III were much shorter, lasting only 14 and 12 weeks, respectively.

Growth Regulators and Fruit Growth

Auxins. Increases in fruit size is mainly a result of cell enlargement. Auxins are often cited as having a dominant role in fruit growth because of their role in cell enlargement (110).

Seeds reportedly produce auxins which move outward toward the carpel wall and stimulate growth (75). Nitsch (75) was able to control the development of strawberry by selectively removing achenes from the receptacle. Where he removed an achene the receptacle did not swell unless he treated the area with a lanolin paste containing β-hydroxyethylhydrazine (BNOA). Gustafson (35) working with tomato showed a concentration gradient of auxins originating in the seeds and extending through surrounding tissues with diminution toward the carpel wall.

There have been numerous correlations of seed number and fruit size (52, 75, 63, 64, 66, 77, 9) and between seeds and fruit shape (1), but there is usually no close correlation between the total amount of auxin produced in seeds and fruit growth (110). Moreover, exogenous applications of auxin have not been as effective as some other growth regulators in bringing about certain growth responses (110).

Gibberellins. Young seeds are a rich source of gibberellin (110, 107). The concentration of gibberellin-like substances in various tissues of apricot fruit correlates closely with growth rates of these tissues throughout fruit development, but not with general fruit growth (47). In 'Seedless Tokay' grape, a close correlation between gibberellin-like activity and berry growth was found during Stages I and II but not in Stage III. The decrease of gibberellin activity in Stage III was attributed to the early cessation of seed development (45). Wiltbank and Krezdorn (121) found positive correlations between concentration of gibberellins in the fruit and rate of fruit growth and also between total gibberellins per fruit and cummulative fruit growth in 'Washington' navel during the first 9 weeks of fruit development.

Commercial application is made of the ability of GA to enlarge the fruits of several grape species (122). 'Thompson Seedless', 'Black Corinth' and 'Delaware' grapes are sprayed commercially with 1 or 2 applications of GA to reduce fruit set, elongate clusters, increase berry size and increase yield.

GA sprays are used to extend the harvest season of sweet cherries and produce larger and firmer fruit that are less prone to growth cracks (122).

GA applications have enhanced fruit size of lemons (14,15), grapefruit (16) and oranges (17, 41), but effects have been variable depending upon time of application, concentration and other factors.

Cytokinins. Cytokinins have been reported to affect fruit size and shape in apples (120); however, others working with different varieties and at other locations have not confirmed this (110). Fruit size was increased in 'Black Corinth' grape (113) using cytokinins but less effect was observed with 'Thompson Seedless' grape (114).

Ethylene. Ethylene is now considered one of the main growth regulators (110). Many plant responses that were formerly believed to result from auxins are now ascribed to ethylene production (8). Growth of the fig fruit is more rapid and the time to maturation shortened by the ethylene produced in the fruit following applications of 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) (67).

Peach diameter was increased by an application of ethephon, an ethylene generator, 4 days before harvest. Application of ethylene or ethephon to grapes during Stage II hastened ripening but benzothiazole-2-oxyacetic acid (BOA), an auxin, retarded ripening during late Stage I or early Stage II. Hale et al.(36) suggested that an auxin-ethylene relationship controls the speed of berry ripening.

Control and Pattern of Movement of Metabolites

There is a preferential movement of metabolites into the phloem following the buildup of assimilates in the photosynthetic tissue of a leaf (109). Sugars, primarily sucrose, constitute most of the organic substances transported in the phloem although nitrogenous substances and

some steroids are also known to be translocated (69, 70, 124, 74, 116, 117, 50, 5, 106). Not only are assimilates selectively moved out of a photosynthesizing leaf into the conducting tissue, but the movement is also done against a concentration gradient (123, 108).

A young expanding leaf obtains carbohydrates from other leaves until it is between 1/3 to 1/2 of its final area, after which time it becomes self-sustaining and begins exporting assimilates (105, 115, 30, 29). Kriedemann (50) reported that a lemon leaf does not become a contributing organ until it is fully mature. The period of maximum export for leaves of several plants occurs soon after they reach full size, the rate subsequently declining with leaf age (13, 100, 109).

There is a pattern of assimilate distribution that applies to most plants. Lower leaves supply assimilates to the roots whereas the upper leaves serve the shoot apex. Assimilates from intermediate leaves may move in either or both directions, depending on demand (85, 109). These patterns have been established on small herbacious plants; however, Hale and Weaver (37) showed much the same pattern with grapes. They demonstrated fewer assimilates were directed toward the apex as the elongating vine grew farther from a given source leaf.

Kriedemann (50) reported an apical flush supporting a lemon fruit directed all photosynthates toward the fruit. There was bidirectional transport in the subapical flush, but acropetal movement predominated. Leaves separated from the fruit by 2 flushes had only basipetal movement. Powell (85) observed the same pattern with seedy 'Calamondin' fruit except that the movement of photosynthates from the apical flush was not entirely acropetal. A slight basipetal movement occurred.

Changing from a vegetative to a fruiting shoot can rapidly alter the pattern of assimilate distribution. A shifting pattern in many cases may be only a change in intensity of assimilate movement in a given direction (109). Work on peas (62), grapes (37), tomato (109) and citrus (50, 85) has shown that a developing fruit has a demand for assimilates from adjacent leaves.

Crane (22) proposed that a high metabolic gradient between the ovary and adjacent vegetative organs is established by the process of fertilization which diverts assimilates toward the developing fruit, even at the expense of vegetative growth. Crafts (20) pointed out that as carbohydrates are transported from their sites of synthesis to those of utilization, other substances including hormones, growth regulators and viruses are also carried along and accumulate in sinks to concentrations that are greater than along the channels of movement.

Crane (22) postulated that the agents which initiate the metabolic gradient come from the ovary and are probably auxins, gibberellins or even cytokinins. He assumed these substances were produced by the seeds or parts of the ovary wall itself.

Later Crane (23) applied auxins, GA, and cytokinins to 'Calimyrna' fig and obtained fruit similar in general morphology and size to those produced by pollination. He concluded that fruit growth is controlled by the ability of growth substances eminating from the seeds to attract metabolites from other regions of the plant. He suggested that the hormones were synthesized in the leaves and stored in the fruit.

The role of growth regulators in mobilization of organic materials has been investigated by exogenous applications of these materials.

Auxins have long been known to increase photosynthate movement to treated areas, and cytokinins have been demonstrated as strong mobilizing agents in leaves (110). IAA, GA_4, GA_7 and BA were applied to apple seedlings to evaluate their ability to mobilize various isotopically labelled substances to treated areas (38). BA mobilized ^{3}H-GA, acropetally and basipetally and mobilization was enhanced by the addition of IAA. An acropetal movement of ^{14}C-kinetin was induced only with a mixture of GA_4, GA_7 and IAA. All of the materials mobilized ^{14}C-sorbitol and ^{14}C-glycine acropetally, and the movement was greatly enhanced by girdling the stem.

Kriedemann (49) applied cytokinins to citrus fruit and thereby enhanced the movement of photosynthate into the fruit. Powell (85) applied GA to 'Calamondin' fruit and observed a pattern of photosynthate distribution that was similar to the strong continuous flow of photosynthates into seedy fruit of that same cultivar. This pattern differed from that of the emasculated controls demonstrating that the endogenous mobilizing force of seeds on photosynthates in 'Calamondin' could be substituted by an exogenous application of GA.

MATERIALS AND METHODS

Plant Material

All plots were located in a 7-year-old 'Washington' navel orchard on sour orange rootstock in Marion County. Fifteen uniform trees were randomly divided into 3 groups of 5 trees each. Approximately 75 flowering shoots with a minimum of 5 new leaves each were selected and tagged on each tree during full bloom. All shoots were thinned to a single large flower at or just prior to anthesis. Shoots selected were all located 1 to 2 M above the ground and in the outer canopy.

Treatments

Treatments consisted of spraying the entire canopy of 1 group of 5 trees with 250 ppm GA and dipping flowers on tagged shoots of the second group in a solution of 250 ppm GA. The third group of trees received no treatment and constituted the control.

No statistical experimental design was used because the objective of the experiment was to study general patterns of movement of metabolites rather than small treatment differences.

$^{14}CO_2$ Exposure

The reaction vessel for generating $^{14}CO_2$ consisted of a 125 ml erlenmeyer sidearm flask fitted with a piece of Tygon tubing, a rubber

septum for a port on the sidearm and a rubber balloon over the top to serve as a diaphragm. The $^{14}CO_2$ was generated by placing 10 mg of Ba $^{14}CO_3$ containing a specific activity of 250 μC in the reaction flask and the diaphragm was sealed over the top. Just prior to fitting the exposure chambers over the leaves, 1 ml of lactic acid was placed in the flask through the port. Care was taken that the lactic acid went through the plastic tubing and did not run down the walls of the flask. The lactic acid was thoroughly mixed with the Ba $^{14}CO_3$ to ensure complete reaction and release of the $^{14}CO_2$. Thirty min were allowed for the reaction to go to completion.

Plastic bags with zipper-like enclosures were modified for use as exposure chambers. The interlocking ridges were removed from the center of the bag for a distance of 5 mm to accomodate the leaf petiole. The space left by removing the enclosure was filled with modeling clay to seal the opening around the petiole and black plastic tape was placed on the lower right side of the bag to make a port for receiving $^{14}CO_2$. Bags for each treatment were color coded and numbered consecutively from 1 to 10.

Two leaves, 1 subtending a tagged spring-flush shoot and 1 selected from near the mid-section of another spring-flush shoot from each tree in each treatment and the control were exposed to $^{14}CO_2$ on each of 19 dates (Table 1). Leaves were exposed to $^{14}CO_2$ during and just prior to the entire fruit-setting period, starting several days before anthesis and continuing until the summer flush of growth was fully expanded and became essentially static.

Table 1. Dates of $^{14}CO_2$ Application to Navel Orange with Reference to Anthesis.

DATE	DAYS AFTER ANTHESIS
4/2/72	-5
4/8/72	1
4/10/72	3
4/13/72	6
4/16/72	9
4/20/72	13
4/24/72	17
4/28/72	21
5/2/72	25
5/8/72	31
5/23/72	46
5/30/72	53
6/17/72	68
6/27/72	81
7/1/72	86
7/5/72	90
7/9/72	94
7/12/72	97
7/17/72	102

The exposure chambers were first placed over all leaves that were to be subjected to $^{14}CO_2$ on a given date. Then, 2.5 ml of $^{14}CO_2$ enriched air containing 5μC specific activity was removed from the reaction flask through the septum and injected through the wall of the exposure chamber with a 5 ml disposable syringe. The black plastic tape was peeled back before injection and replaced afterwards to seal the hole left by the needle.

Injection of $^{14}CO_2$ into all of the bags required 10 min hence the starting time for all replicates was approximately the same. Exposure to $^{14}CO_2$ began on each date at 8:30 AM and continued until 12:30 PM. Shoots were harvested after the 4-hr exposure, and the exposed leaf of each shoot was removed and placed in a coded envelope. Each shoot and the envelope containing the exposed leaf were placed in a paper bag and immediately frozen with dry ice. Samples were subsequently stored at -20C until analyzed. Shoots were harvested in the same order they were exposed to $^{14}CO_2$.

Analyses

Frozen plant material from shoots harvested on 19 designated dates (Table 1) was taken to the laboratory where the shoots were immediately dissected, placed in coded envelopes, and restored at -20°C. Shoots in which old leaves were exposed were dissected into 1) ovary (flower or fruit), 2) exposed leaf, 3) leaves, and 4) stem (Fig. 1). Shoots with a new median leaf exposed were divided into 1) ovary, 2) exposed leaf, 3) leaves distal to exposed leaf, 4) stem distal to exposed leaf, 5) leaves basal to exposed leaf, 6) stem basal to exposed leaf, and 7) old basal leaf from a previous growth flush (Fig. 2).

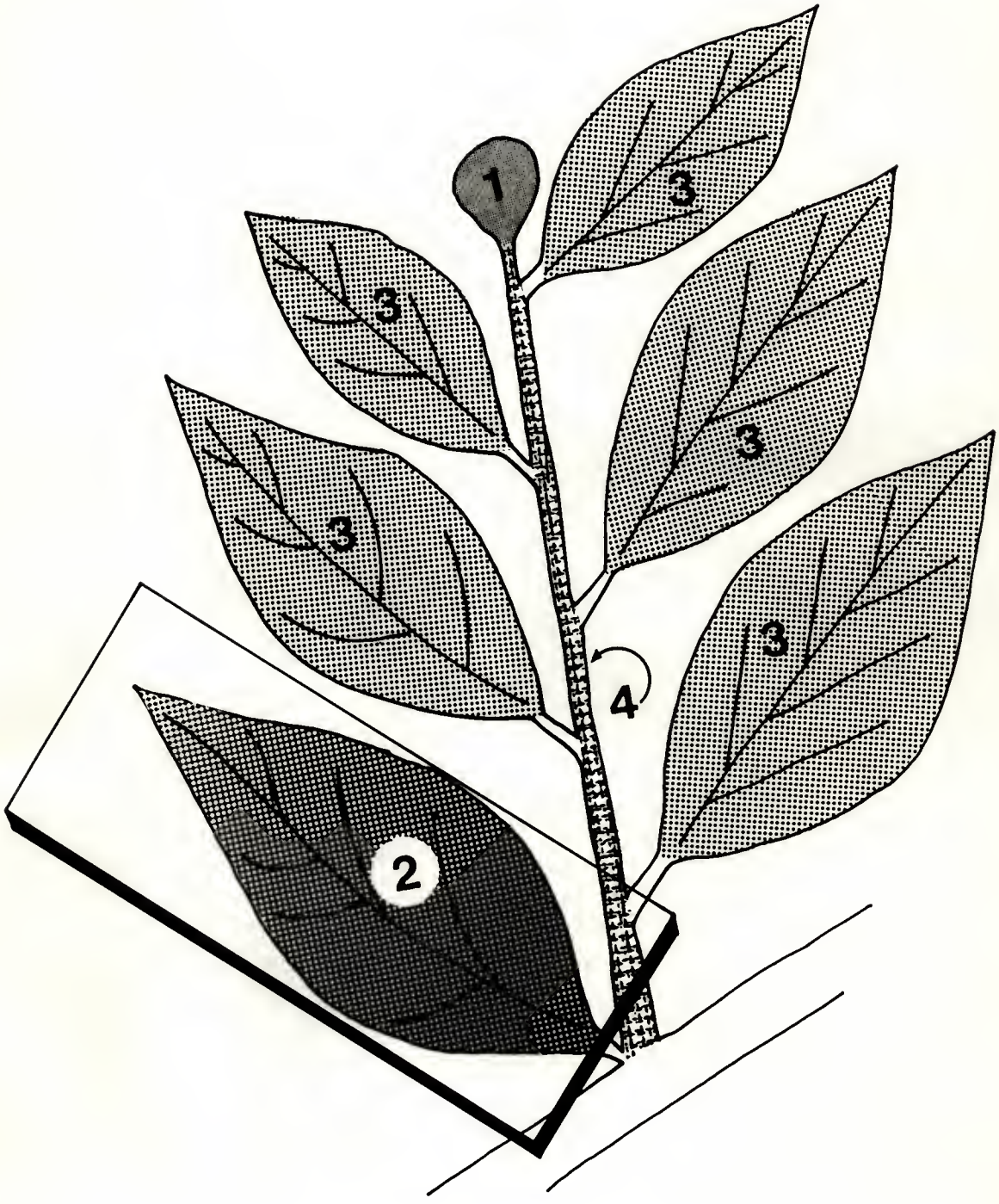

Fig. 1. Diagramatic sketch of shoot showing position of leaf exposed to $^{14}CO_2$. Differing numbers indicate subsamples after treatment, namely, 1) ovary (flower or fruit) 2) exposed leaf 3) leaves 4) stem

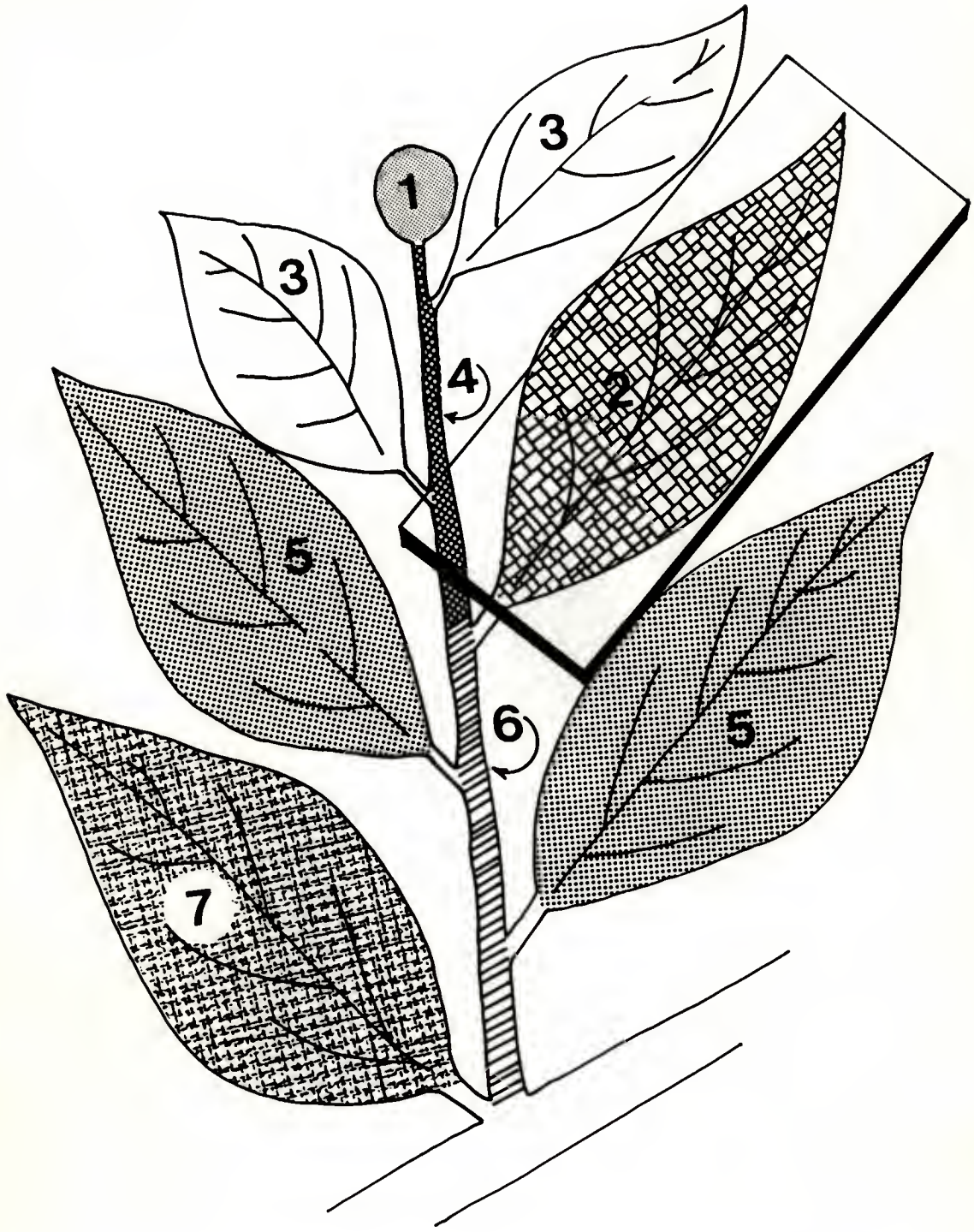

Fig. 2. Diagramatic sketch of shoot showing position of leaf exposed to $^{14}CO_2$. Differing numbers indicate subsamples after treatment, namely, 1) ovary (flower or fruit) 2) exposed leaf 3) leaves distal to exposed leaf 4) stem distal to exposed leaf 5) leaves basal to exposed leaf 6) stem basal to the exposed leaf 7) subtending leaf from a previous flush

Samples were removed from storage and dried in a forced draft oven for 48 hrs. Fruit larger than 2.5 cm in diameter were dried separately for 72 hrs.

Each sample was crushed, mixed thoroughly and dry wt determined. A 100-mg aliquot was taken. Fruits heavier than 100 mg were ground in a Wiley mill through a 40-mesh screen before removing the aliquot.

Several methods of preparing samples for scintillation counting were attempted including oxidation in a Schönonger flask and dissolving the plant material in various tissue solubilizers. Oxidation in a Schönonger flask was a bulky procedure and was not suited to handling large numbers of samples.

Tissue solubilizers all resulted in highly colored solutions due to chlorophyll pigments contained in the plant tissues. This caused severe quenching of ^{14}C-counts when counted in a liquid scintillation spectrophotometer. Attempts to use bleaching agents to remove the color were unsuccessful due to quenching from the bleach. Quenching curves were constructed, but the amount of quenching was so large that reliable data could not be obtained.

Automated oxidation assemblies were available, but their cost was prohibitive, so an oxidation train (Fig. 3) was constructed.

The apparatus consisted, in part, of a brass tube which was connected to an O_2 source by Tygon tubing on 1 end and contained a nichrome sample basket on the other. The O_2 tube and sample basket were screwed into another tube to create a closed system for oxidation. The tube was heated and an O_2 flow of 1 L/min was passed through the system allowing for complete oxidation of the sample and sweeping the oxidation products through the system. Heat was supplied by a Bunsen burner placed under

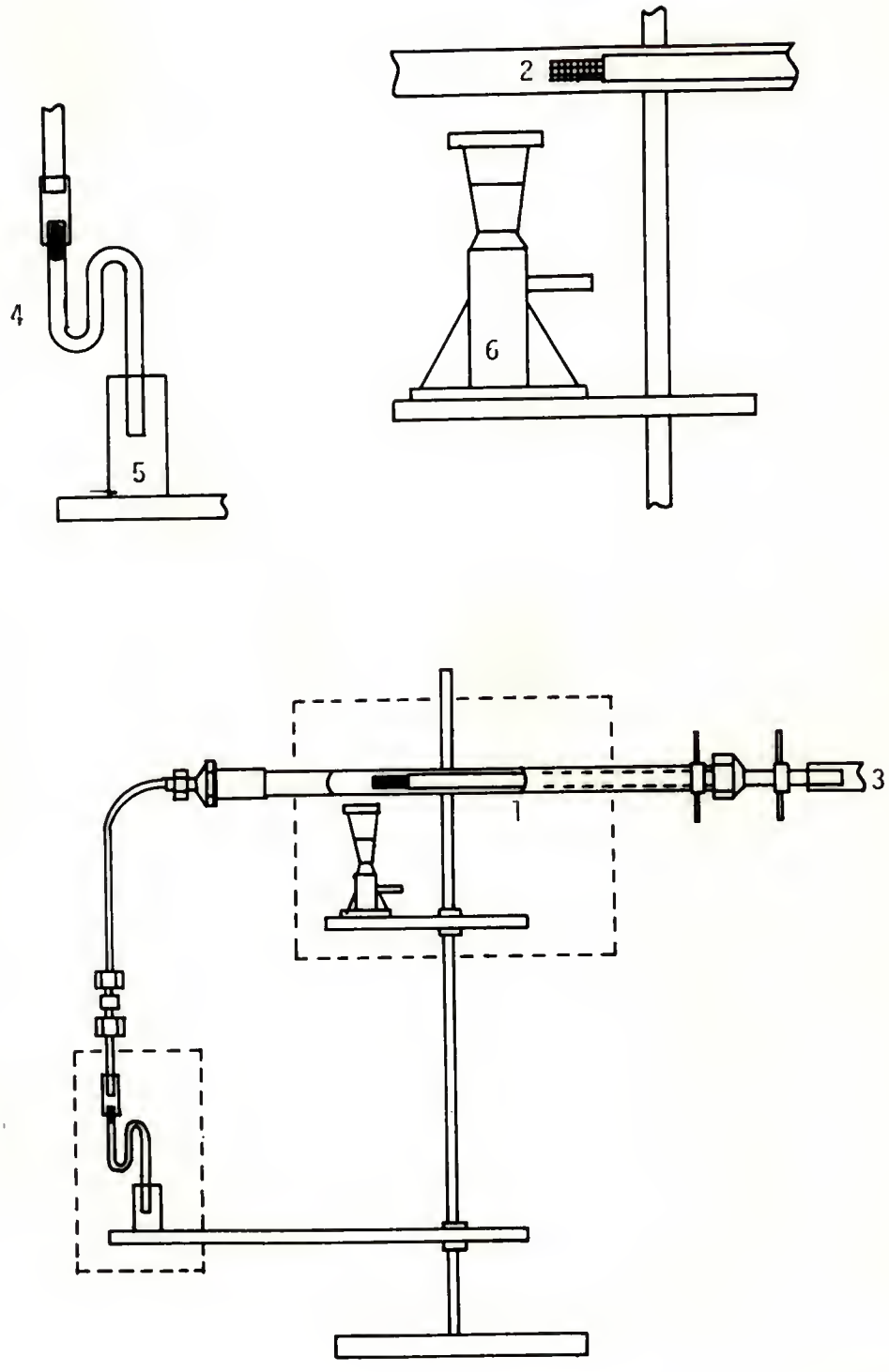

Fig. 3. Diagram of apparatus used to oxidize plant material and trap the resulting $^{14}CO_2$. It consisted of: 1) oxidation tube 2) sample basket 3) oxygen tube 4) water trap 5) vial containing phenethylamine, a CO_2 trapping agent 6) Bunsen burner

the oxidation tube immediately behind the location of the sample basket inside. The location was critical. Placing heat directly under the basket heated the sample slowly and caused unoxidized material to be driven off briefly before ignition of the sample. Placing heat too far behind the sample delayed ignition, but by locating heat just behind the sample, the walls of the tube became very hot and anything driven off before ignition passed through this area and was oxidized. Glass tubing was bent to create a water trap and the tip was drawn out in order to scrub the CO_2 from the oxidation products as they passed through the phenethylamine, contained in a scintillation vial.

A sample was wrapped tightly in cigarette paper and placed in the sample basket for oxidation. The flow of O_2 was started and the O_2 tube and basket were screwed into the oxidation tube. A scintillation vial containing 15 ml of scintillation solution was placed under the bubbling tube to trap the oxidation products and the Bunsen burner was ignited. Ignition of the sample was viewed through the end of the O_2 tube which was connected to Tygon tubing. Oxidation lasted approximately 15 sec and the system was flushed with O_2 for 40 sec after oxidation was complete. The scintillation vial containing the oxidation products was removed before the O_2 flow was stopped which kept the inside of the tube free of any scintillation solution to facilitate cleaning.

Samples were oxidized systematically by running replicates and cleaning the system after each set of 5 replicates. Cleaning was accomplished by blowing out the train with air, washing the water trap with ethyl alcohol and replacing the glass wool filter.

Samples for each ^{14}C exposure date were arranged in a Packard Tri Carb model 3380 liquid scintillation spectrophotometer with replicates of each treatment consecutive. The ^{14}C preset channel was used and an automatic external standardization ratio was determined for each sample, which provided a comparison of the relative quenching between samples. Each sample was counted for 5 min.

RESULTS

Leaf Dry Weight

Dry wts of leaves increased until 25 days after anthesis but there were no differences due to treatments (Fig. 4). Dry wts of leaves from GA-sprayed trees were greater than for the other 2 treatments, from 46 days after anthesis until the termination of the experiment. Leaves from shoots dipped in GA were intermediate in dry wt between the control and the GA-sprayed treatment.

Fruit Dry Weight

Mean dry wts of fruit from all treatments were similar at anthesis and for several days thereafter (Table 2). Thirteen days after anthesis, however, dry wts of GA-dip fruit had become noticeably greater than those for the GA-spray treatment and the control, and their difference was maintained until 86 days after anthesis. Dry wts of fruit from the control trees were much greater than for the GA-spray treatment 31 days after anthesis. The GA-dip fruit did not vary greatly from the control from 86 days after anthesis until the conclusion of the experiment, but the dry wt of fruit from both the control and the GA-dip treatments remained greater than for fruit from the GA-spray treatment until the termination of the experiment.

Dry wts of fruit from the control were initially less than those of the GA-dip treatment, but appeared to catch up toward the end of the experiment. This was probably due to the manner of determining dry wt

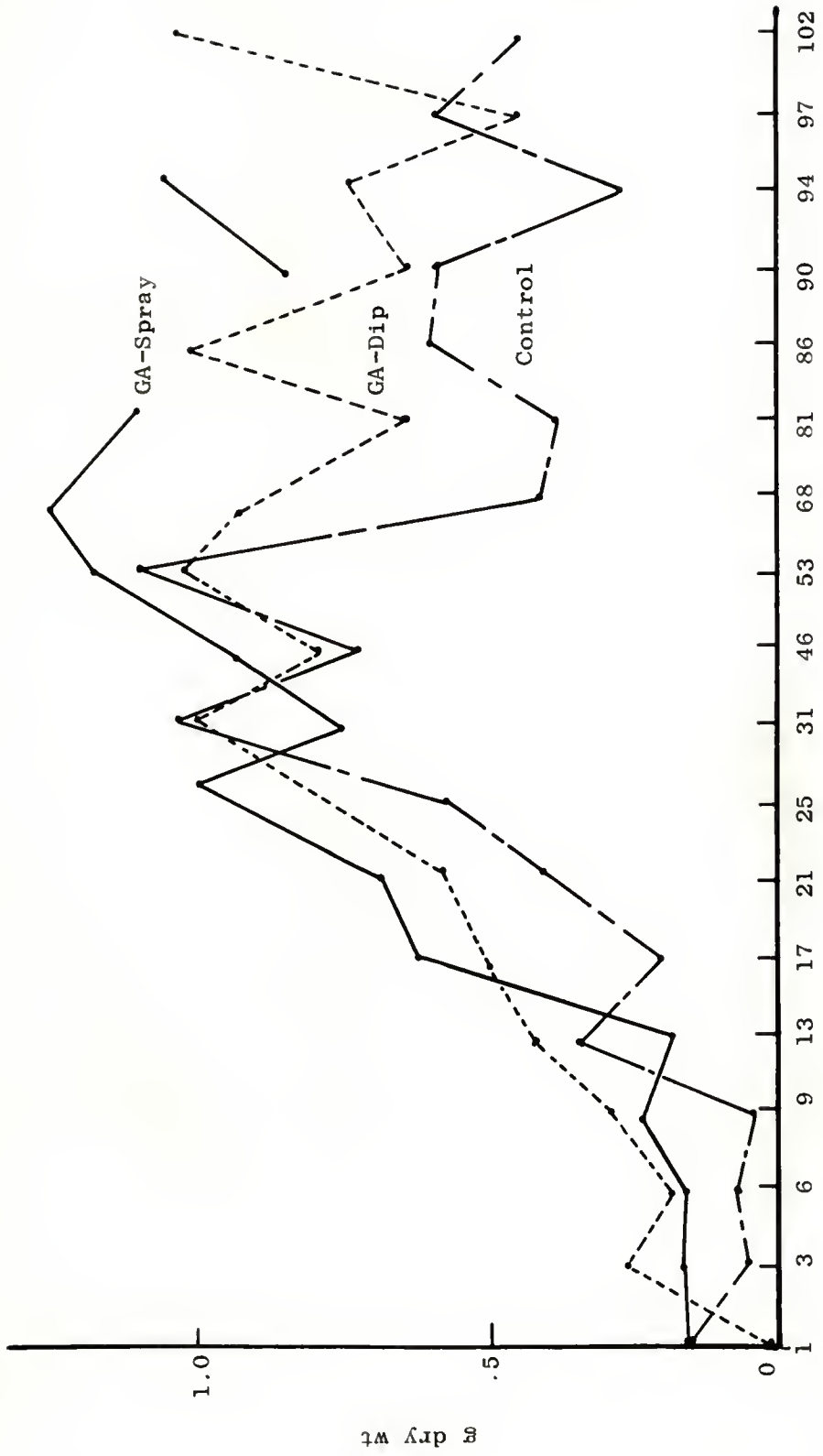

Fig. 4. Comparison of mean dry wts/shoot of navel orange as affected by GA treatments.

Table 2. Comparison of mean dry wts of fruits dipped in GA, fruits from whole trees sprayed with GA and untreated controls.

Days after Anthesis	Dry Wt. (mg)		
	Control	GA-Dip	GA-Spray
-5	56		
1	113	124	118
3	134	124	127
6	148	149	138
9	130	141	127
13	134	189	150
17	186	261	169
21	339	416	240
25	317	822	287
31	1223	3350	711
46	4441	7200	2202
53	8358	9377	3384
68	19,523	21,597	11,459
81	21,987	26,300	15,824
86	29,243	26,922	------
90	32,502	25,934	17,686
94	34,596	35,016	19,509
97	35,937	34,946	------
102	37,182	38,688	------

of the fruit. Fruit harvested for ^{14}C-analysis on each date were used for dry wt determinations. Initially, fruit of all degrees of ability to survive were in the lot sampled, but as the experiment progressed, only the larger more competitive fruit of the control survived, leaving only the largest fruit for experimental use.

^{14}C-Distribution

Fruit. The importation of ^{14}C-photosynthates into the fruit from the median leaf on the shoot increased up to the 17th day after anthesis in both the control and the GA-spray treatments (Fig. 5), as indicated by increases in concentration of ^{14}C in the fruit. The concentration of ^{14}C in the fruit decreased gradually the next 14 days and became almost negligible by 68 days after anthesis. Fruit from the GA-dip treatment had an increase in ^{14}C concentration which peaked at the same time as the other treatments, but remained high for 14 days before declining. The concentration of ^{14}C in the GA-dip treatments also became negligible by 68 days after anthesis.

Concentrations of ^{14}C derived from a median leaf in the fruit from the control and GA-spray treatments were similar throughout the experiment, but concentrations of ^{14}C in fruit from GA-dip treatments were generally higher than for other treatments for 58 days after anthesis. Concentrations of ^{14}C in fruit from all treatments were similar and extremely low during the last 34 days of the experiment, caused primarily by a dilution effect due to substantial increases in fruit size.

Concentrations of ^{14}C-photosynthate exported from a leaf of a previous growth flush into fruits of all treatments were very strong at anthesis and decreased each date until 68 days after anthesis after which

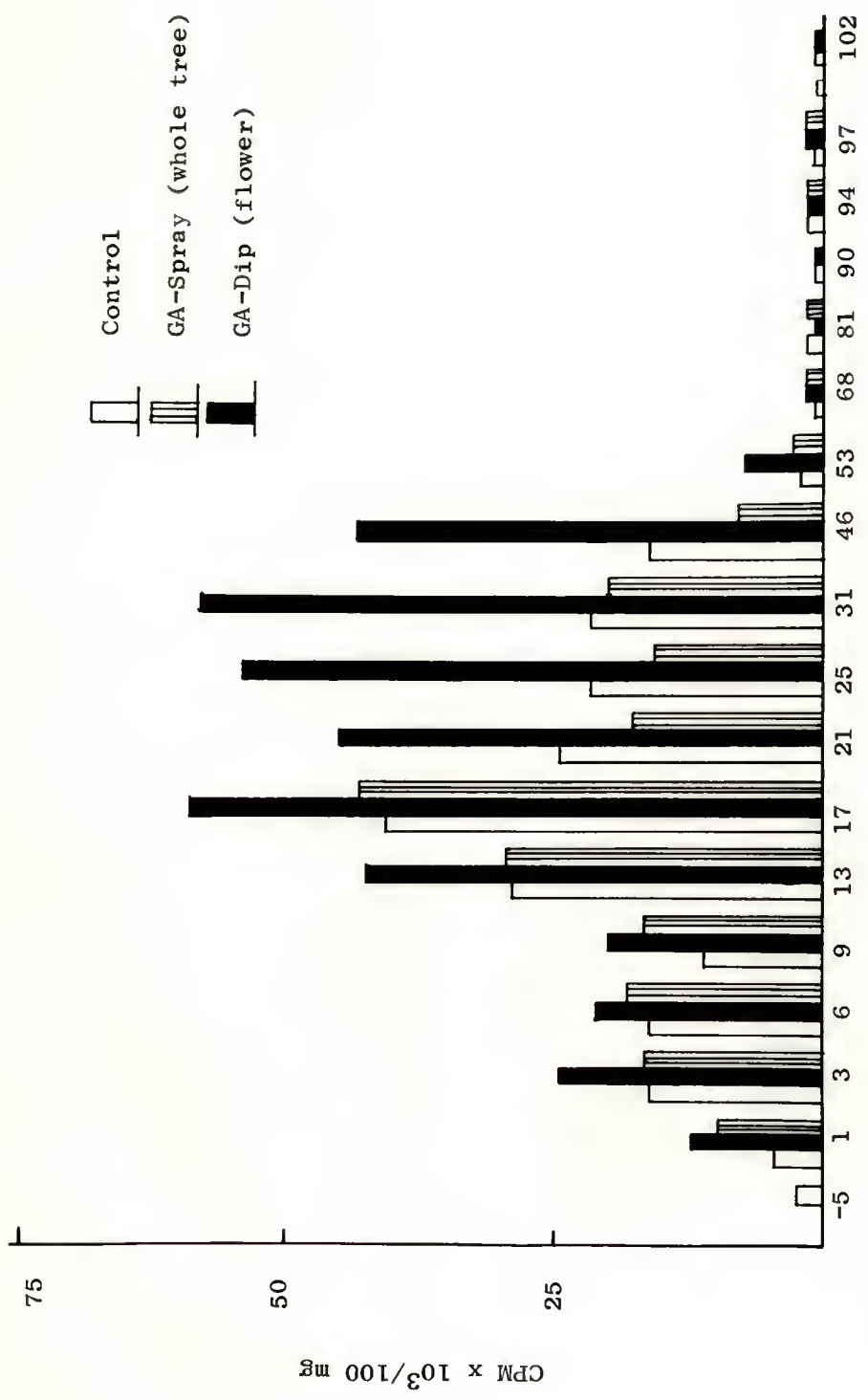

Fig. 5. Comparison of translocation patterns of ^{14}C photosynthates from a median leaf to the fruit during fruit set as influenced by GA treatments.

^{14}C-photosynthate concentration was minimal (Fig. 6). The pattern of ^{14}C-labelled photosynthate movement into fruits of the control and the GA-spray treatments were very similar on each date but movement of labelled photosynthate in the GA-dip treatment became substantially stronger by 6 days after anthesis. The movement of ^{14}C-photosynthate into the GA-dip fruit remained strong until movement from the newly formed leaves became strong, as Powell (85) found in 'Calamondin.'

Seasonal patterns of movement of ^{14}C-labelled photosynthate to the fruit differed from those portrayed on a dry wt basis, because the dilution effect due to increase in fruit size was taken into consideration. The total importation of ^{14}C from an old basal leaf to the fruit had 3 main peaks during the course of the experiment: a) at anthesis, b) at 53 days after anthesis, and c) at 97 days after anthesis (Fig. 7). In general, the strongest movement was sustained by the GA-dip treatment except for a period of 26 days, from 68 to 94 days after anthesis, when the total movement was stronger into the control and GA-sprayed fruit than into GA-dip fruit.

Total movement of labelled photosynthate from the new median leaf to the fruit followed the same general pattern as from the leaf of a previous growth flush (Fig. 8). There was generally a greater difference between the concentration of ^{14}C-labelled metabolites in fruit from the GA-dip and the other treatments when the ^{14}C was derived from a new leaf than when the source leaf was from a previous growth flush. Also there was not a corresponding period in which the GA-dip fruit accumulated less total ^{14}C photosynthates than the other treatments as was found from the "old" source leaf.

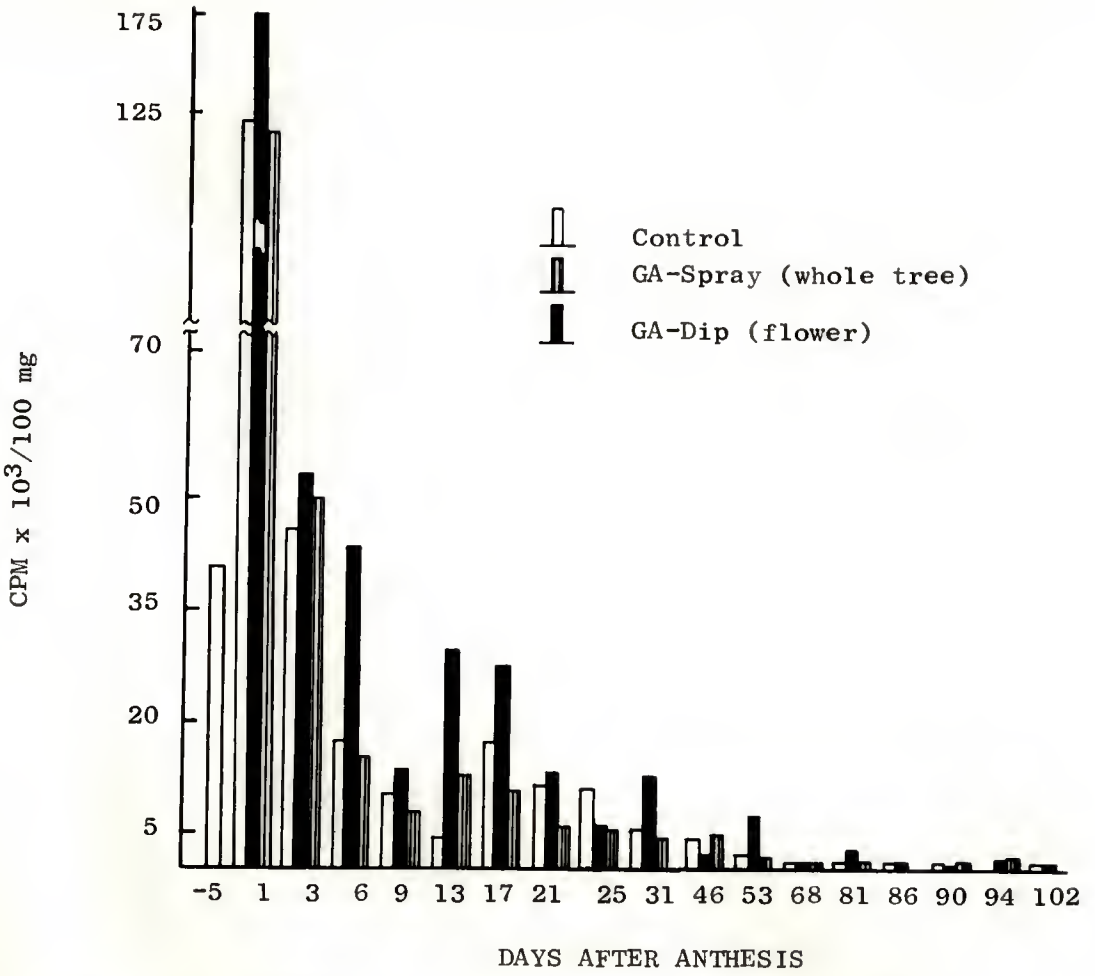

Fig. 6. Comparison of translocation patterns of ^{14}C photosynthate from a basal leaf of a previous flush to the fruit during fruit set as influenced by GA treatments.

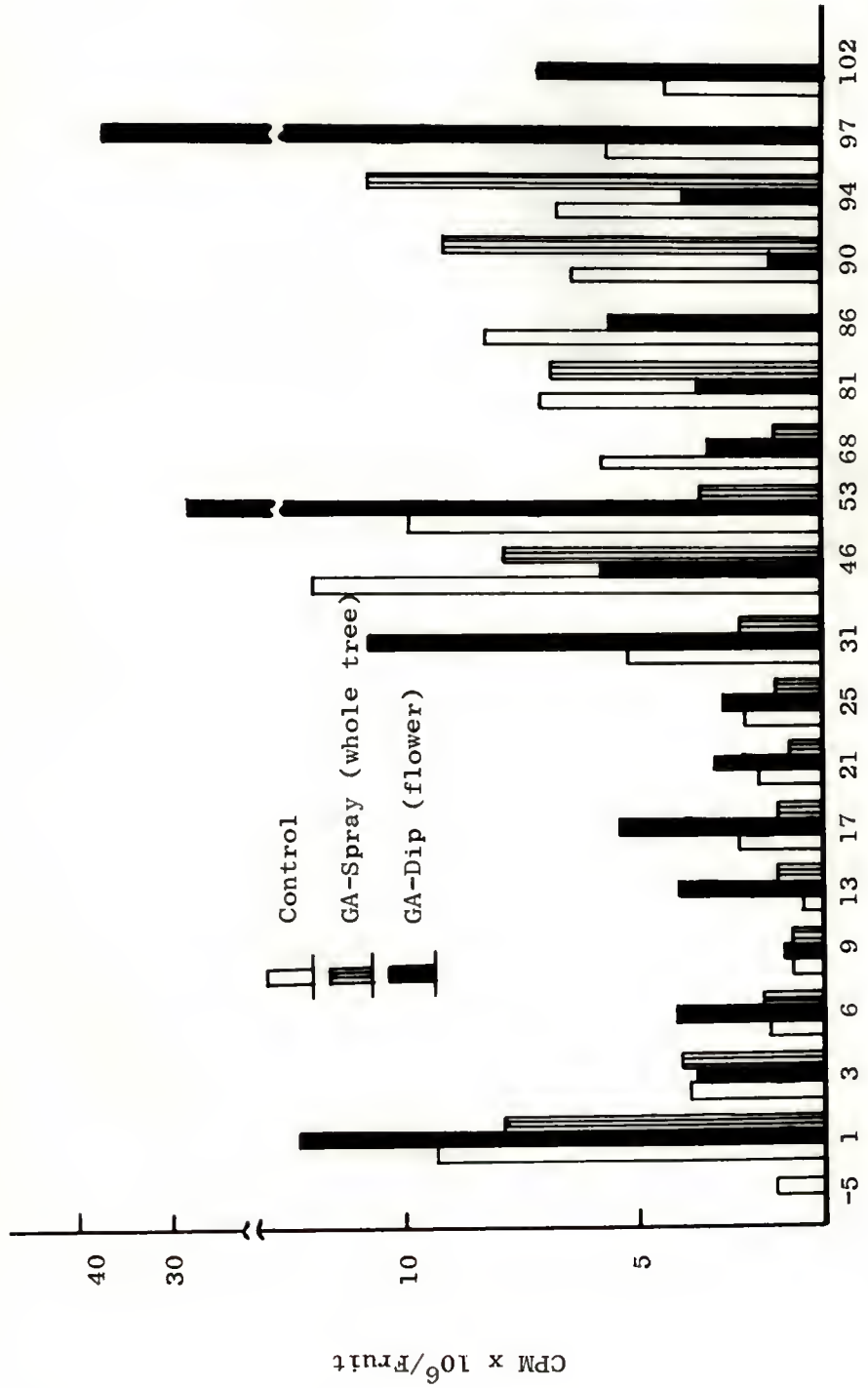

Fig. 7. Comparison of translocation patterns of ^{14}C photosynthate from a basal leaf of a previous flush to the fruit during fruit set as influenced by GA treatments.

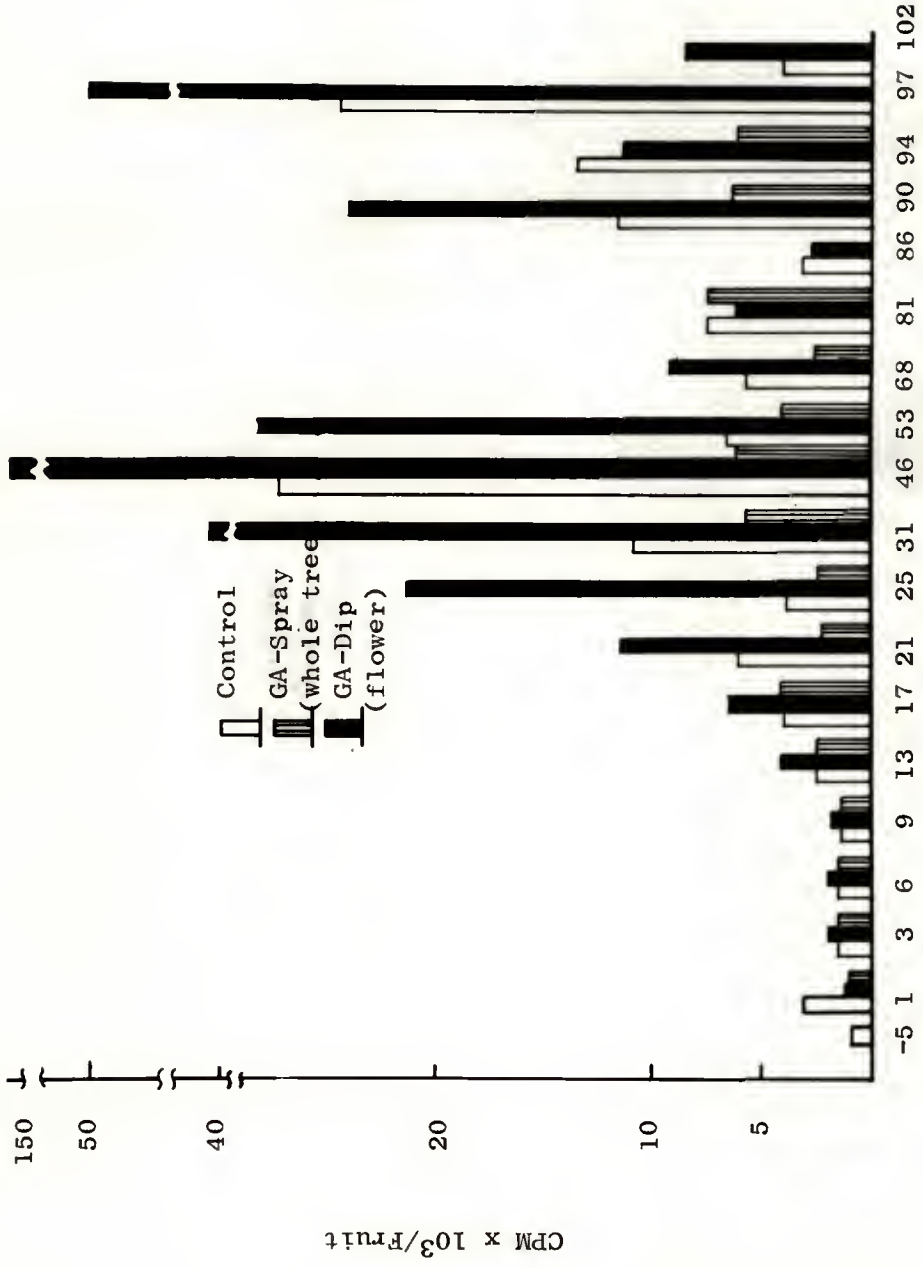

Fig. 8. Comparison of translocation patterns of ^{14}C photosynthate from a median leaf to the fruit during fruit set as influenced by GA treatments.

There was a short interval just before the expansion of the summer flush in which fruit from all treatments had a period of reduced importation of photosynthates. This agrees with other work on citrus and shows a competition between newly developing leaves and fruit for current photosynthates (85).

Leaves. The movement of ^{14}C-metabolites from a median leaf on the shoot was primarily acropetal regardless of treatment or date (Fig. 9). Movement from a median leaf into leaves distal to it became successively stronger for all treatments from anthesis until 9 days later and then decreased for a period of 14 days. Then, the general trend was for the movement of labelled metabolites in all treatments to become stronger again, with a peak about 68 days after anthesis. Movement of labelled metabolites for the GA-dip and GA-spray treatment then decreased until a level similar to the acropetal movement prior to anthesis was reached. Movement of labelled photosynthates from the median leaf of the control increased substantially 97 days after anthesis then decreased on the final date of monitoring to a level twice the GA-dip treatment.

The basipetal movement of ^{14}C-photosynthates from a median leaf to other leaves of the same flush was fairly uniform throughout the experiment for all treatments (Fig. 10). There was a slight increase in photosynthate movement in the GA-dip treatment over other treatments from 13 days to 46 days after anthesis.

Photosynthate movement from a median leaf into a leaf of a previous growth flush was fairly constant until 90 days after anthesis, at which time the movement from the GA-dip treatment was many times greater than the control or GA-spray treatment (Fig. 11). This time period corresponded with the expansion of the summer growth flush.

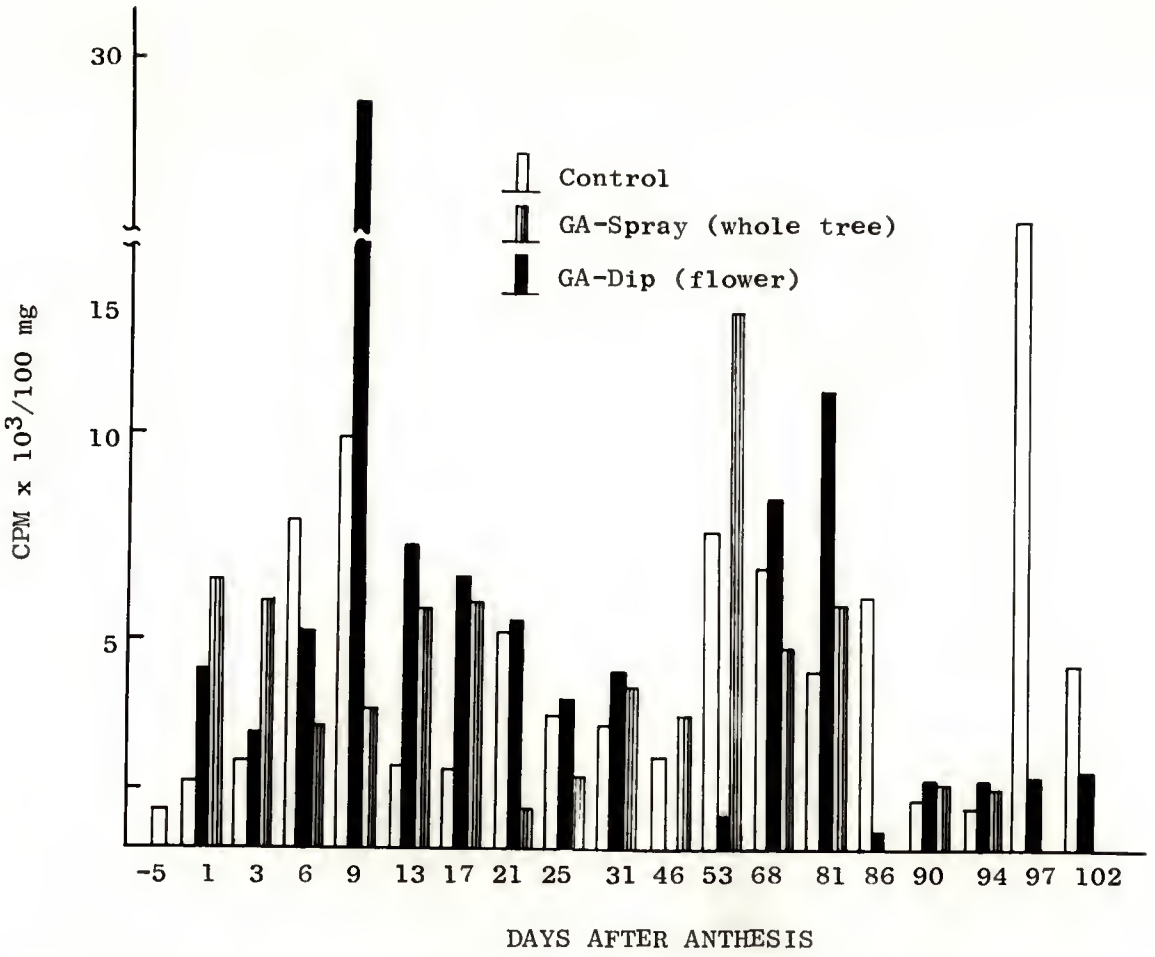

Fig. 9. Comparison of translocation patterns of ^{14}C photosynthate from a median leaf to leaves distal to the exposed leaf during fruit set as influenced by GA treatments.

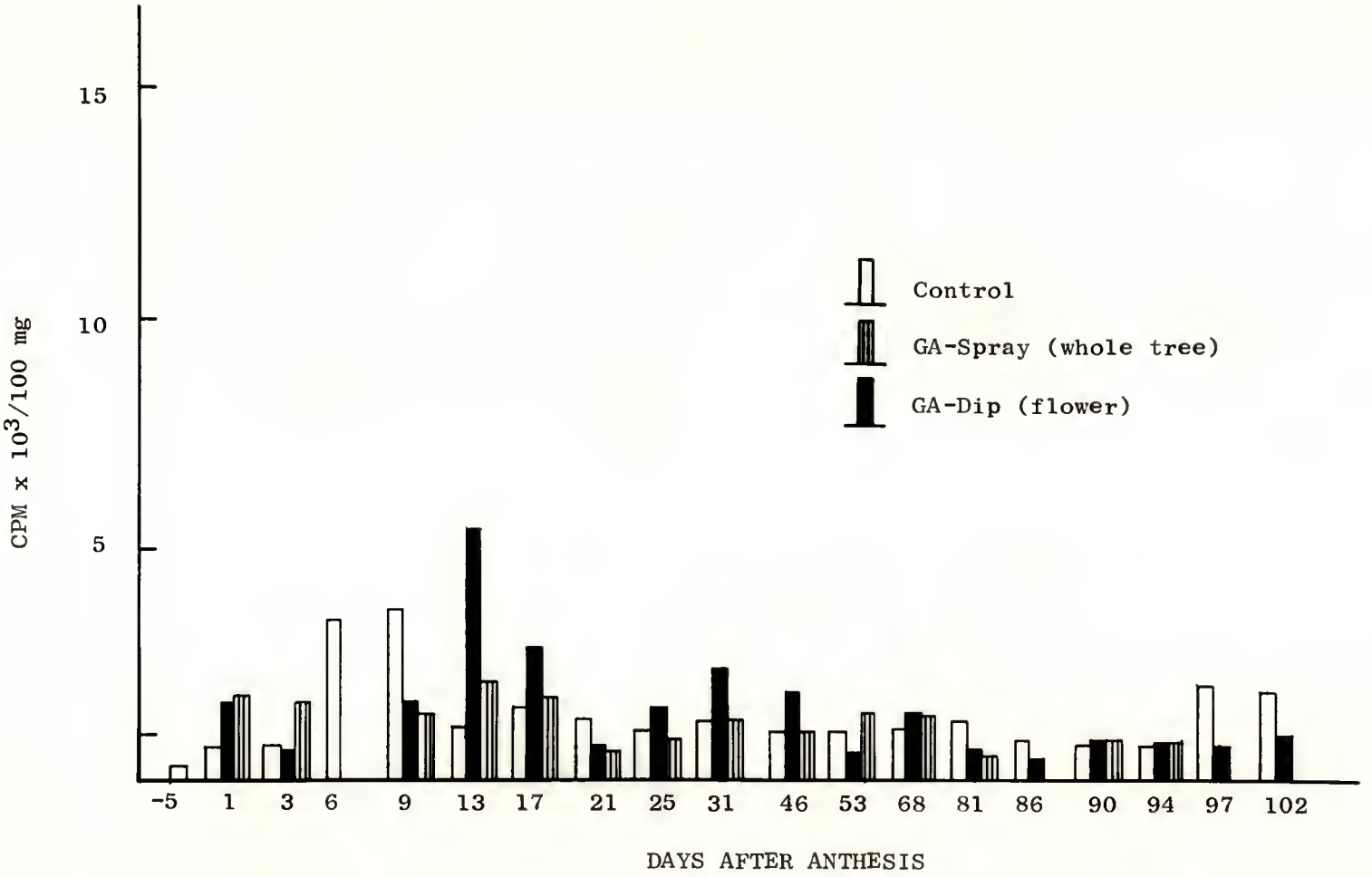

Fig. 10. Comparison of translocation patterns of ^{14}C photosynthate from a median leaf to leaves basal to the exposed leaf during fruit set as influenced by GA treatments.

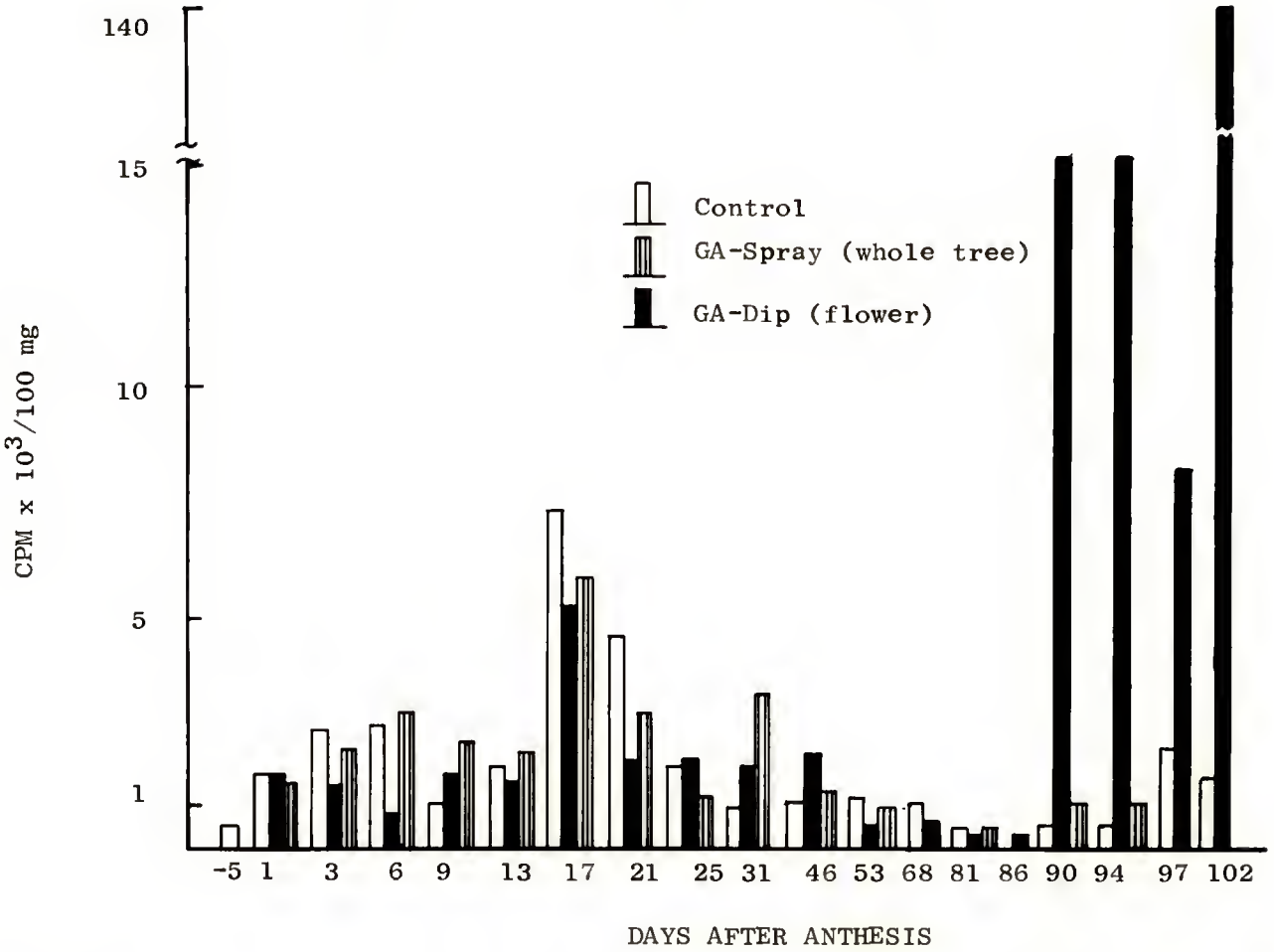

Fig. 11. Comparison of translocation patterns of ^{14}C photosynthate from a median leaf to a subtending leaf of a previous flush during fruit set as influenced by GA treatments.

The pattern of movement of ^{14}C-labelled photosynthates from the leaf subtending the current - season shoot into the leaves of that shoot was similar to the pattern of ^{14}C-photosynthate movement to the fruit (Fig. 12). The movement was strong until shortly after anthesis and gradually decreased to 13 days after anthesis. All treatments remained constant until 46 days after anthesis, at which time there was an upward trend similar to the acropetal movement from the median leaf.

Beginning 3 days after anthesis and lasting 6 days, ^{14}C-photosynthate movement from the previous flush leaf into the leaves of the new flush was much stronger for the GA-spray treatment than for the others.

The ^{14}C-photosynthate movement from the previous flush leaf into the new leaves became substantially greater in the GA-dip treatments than in either the control or the GA-spray treatments, toward the end of the experimental period when the summer leaf flush began emerging.

Stem. Movement of ^{14}C in the stem apical to the median leaf that was exposed to the $^{14}CO_2$ was essentially the same as that from the median leaf to the fruit for all treatments (Fig. 13). The basal portion of the stem retained substantial concentrations of ^{14}C for all treatments from 13 days until 46 days after anthesis (Fig. 14). The stem of the new flush retained ^{14}C derived from an old leaf at the base of the flush similar to the importation of ^{14}C by the fruit from the same source leaf (Fig. 15).

Exposed Leaves. The general trend of ^{14}C retention by the new leaves was that which might be anticipated (Fig. 16). There was a strong retention of ^{14}C by all treatments at anthesis and as the leaves matured they exported a larger portion of the labelled photosynthates.

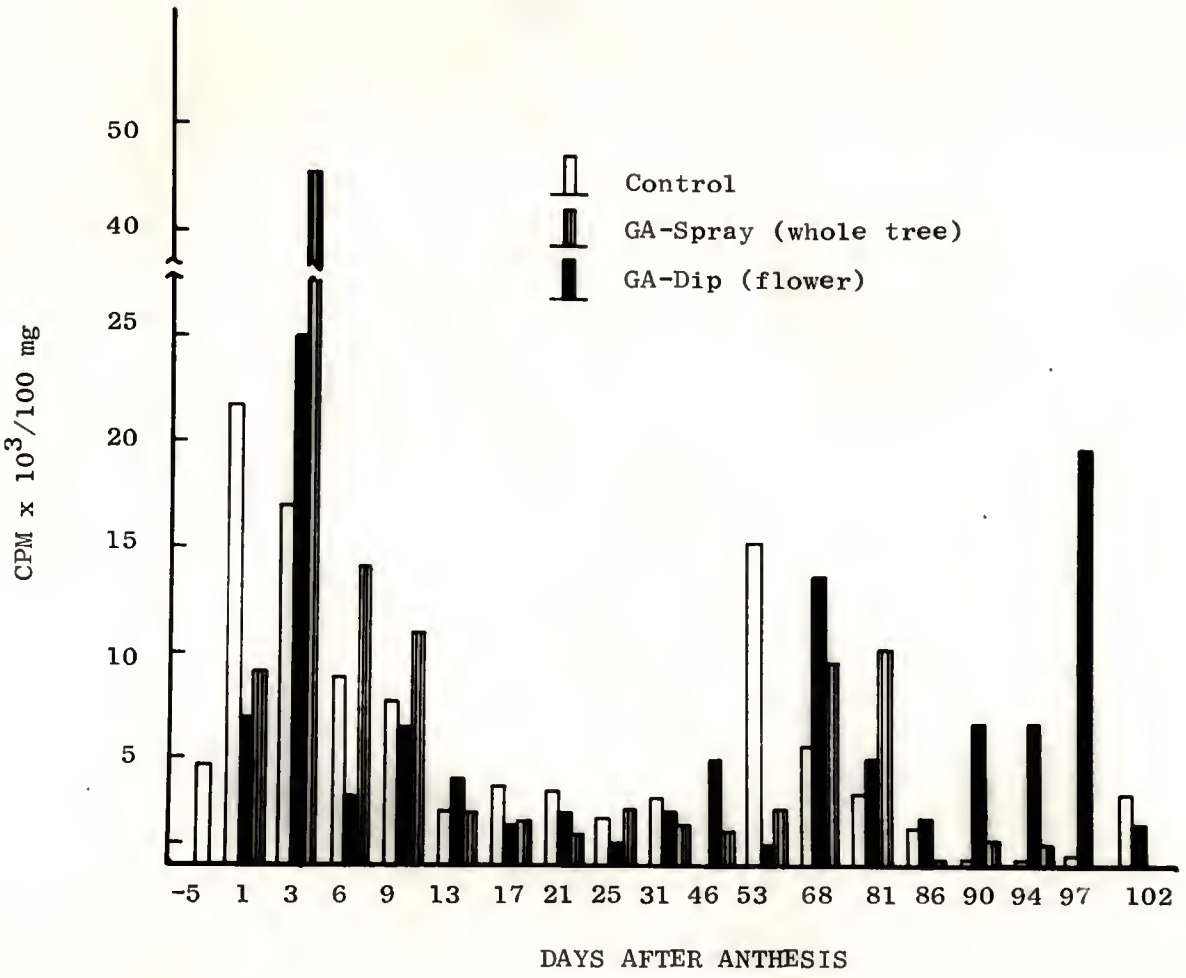

Fig. 12. Comparison of translocation patterns of ^{14}C photosynthate from a subtending leaf of a previous flush to leaves of the new flush during fruit set as influenced by GA treatments.

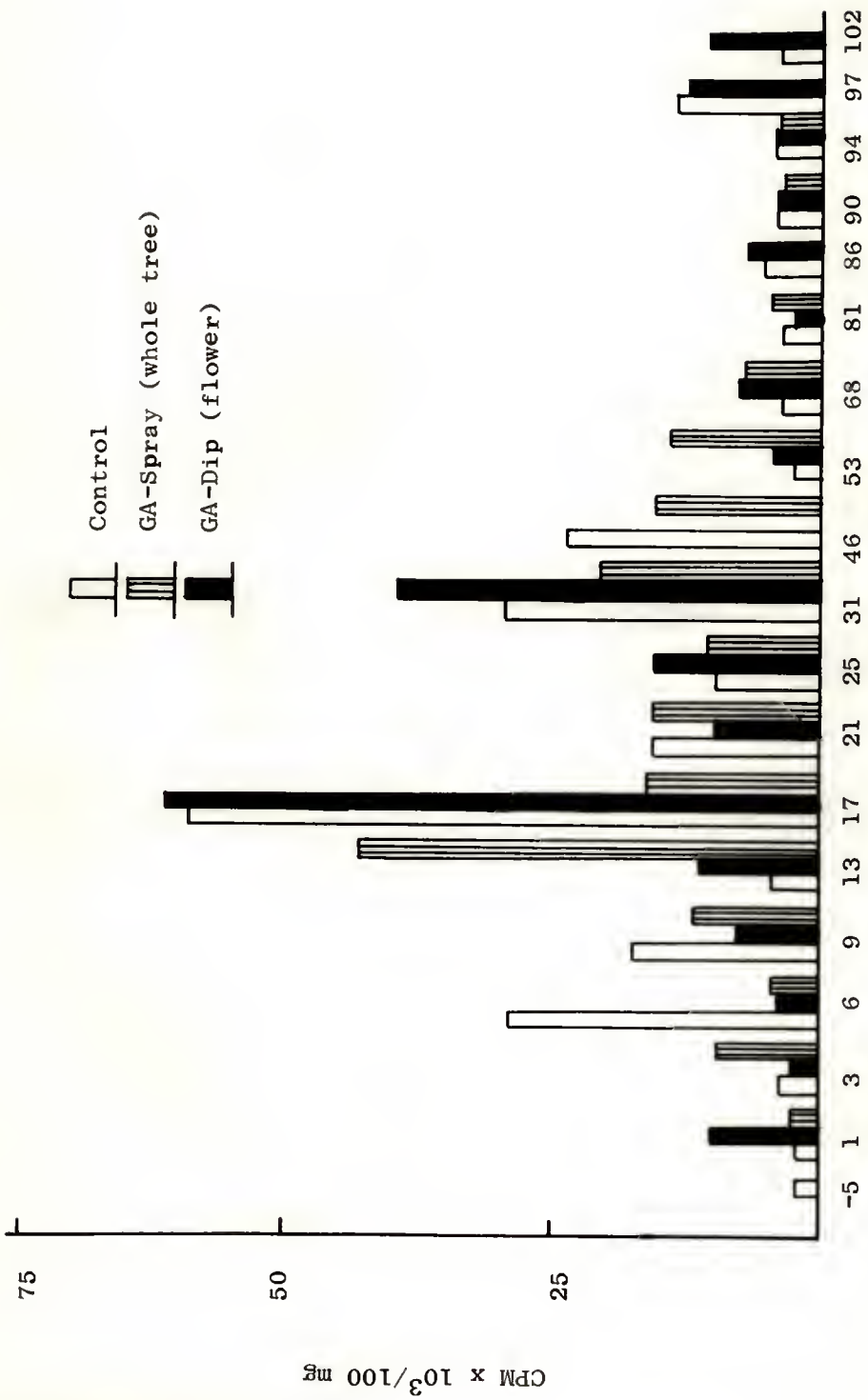

Fig. 13. Comparison of translocation patterns from a median leaf to the stem distal to the exposed leaf during fruit set as influenced by GA treatments.

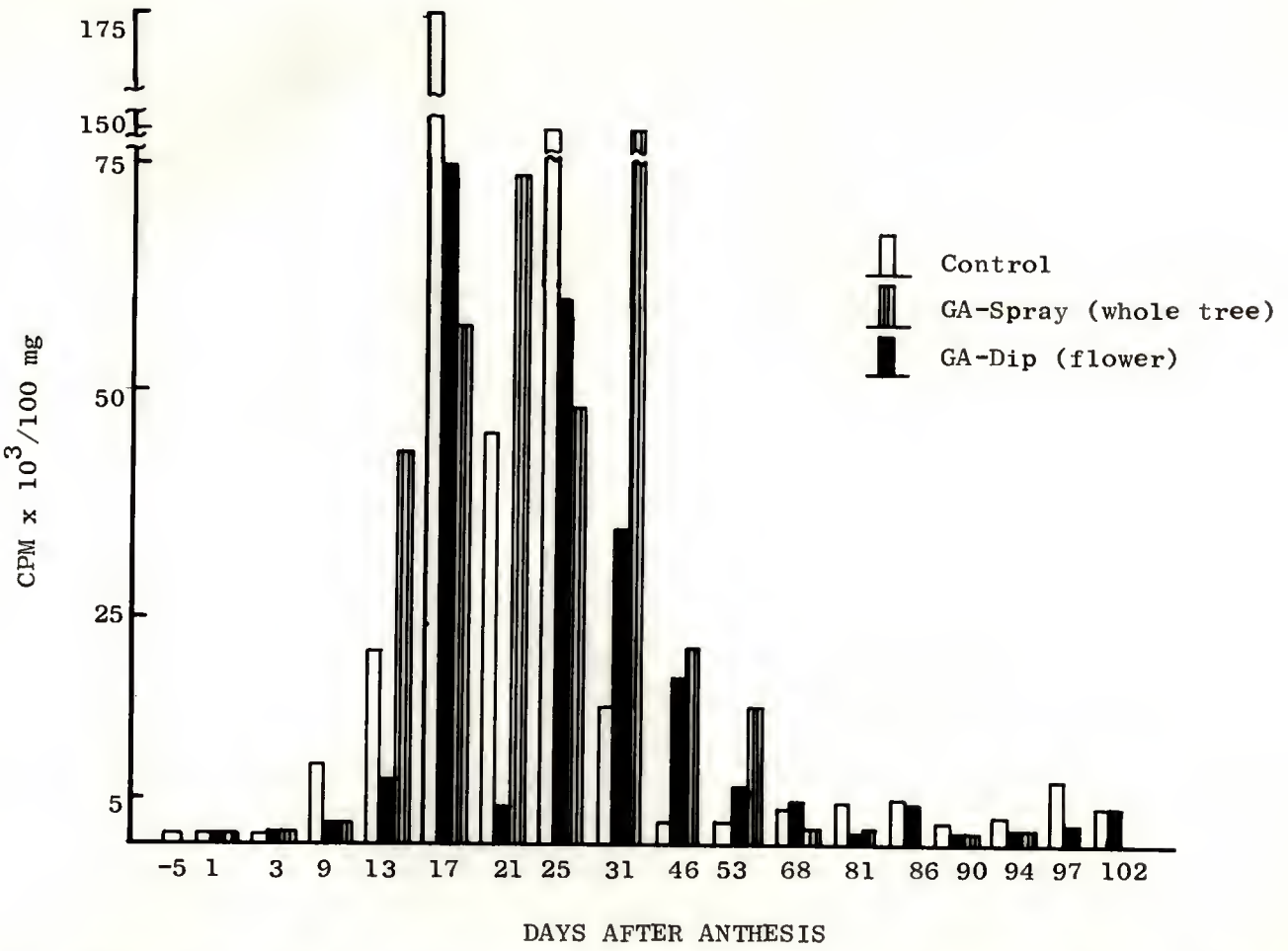

Fig. 14. Comparison of translocation patterns of ^{14}C photosynthate from a median leaf to the stem basal to the exposed leaf during fruit set as influenced by GA treatments.

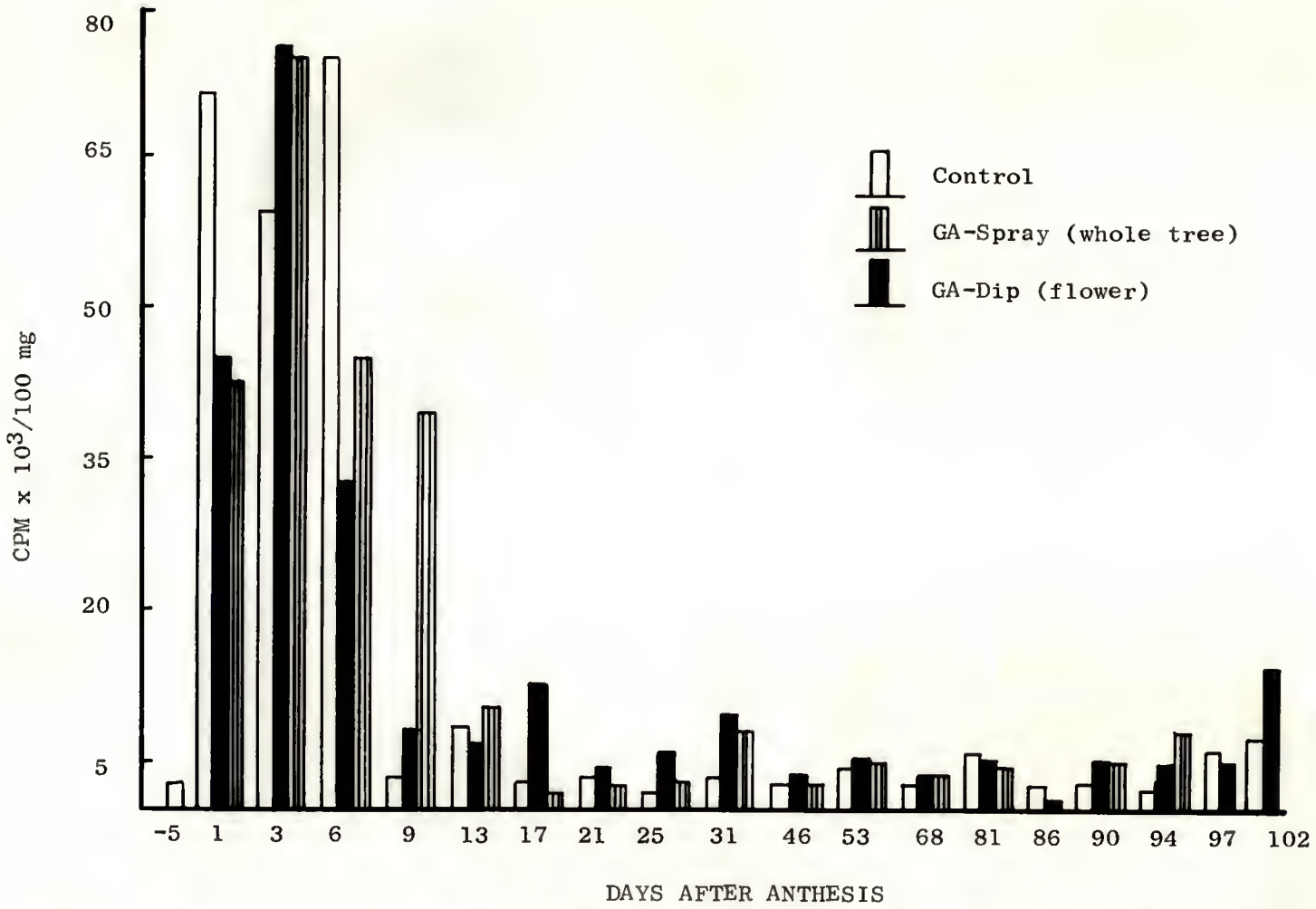

Fig. 15. Comparison of translocation patterns of ^{14}C photosynthate from a subtending leaf of a previous flush to the stem of the new flush during fruit set as influenced by GA treatments.

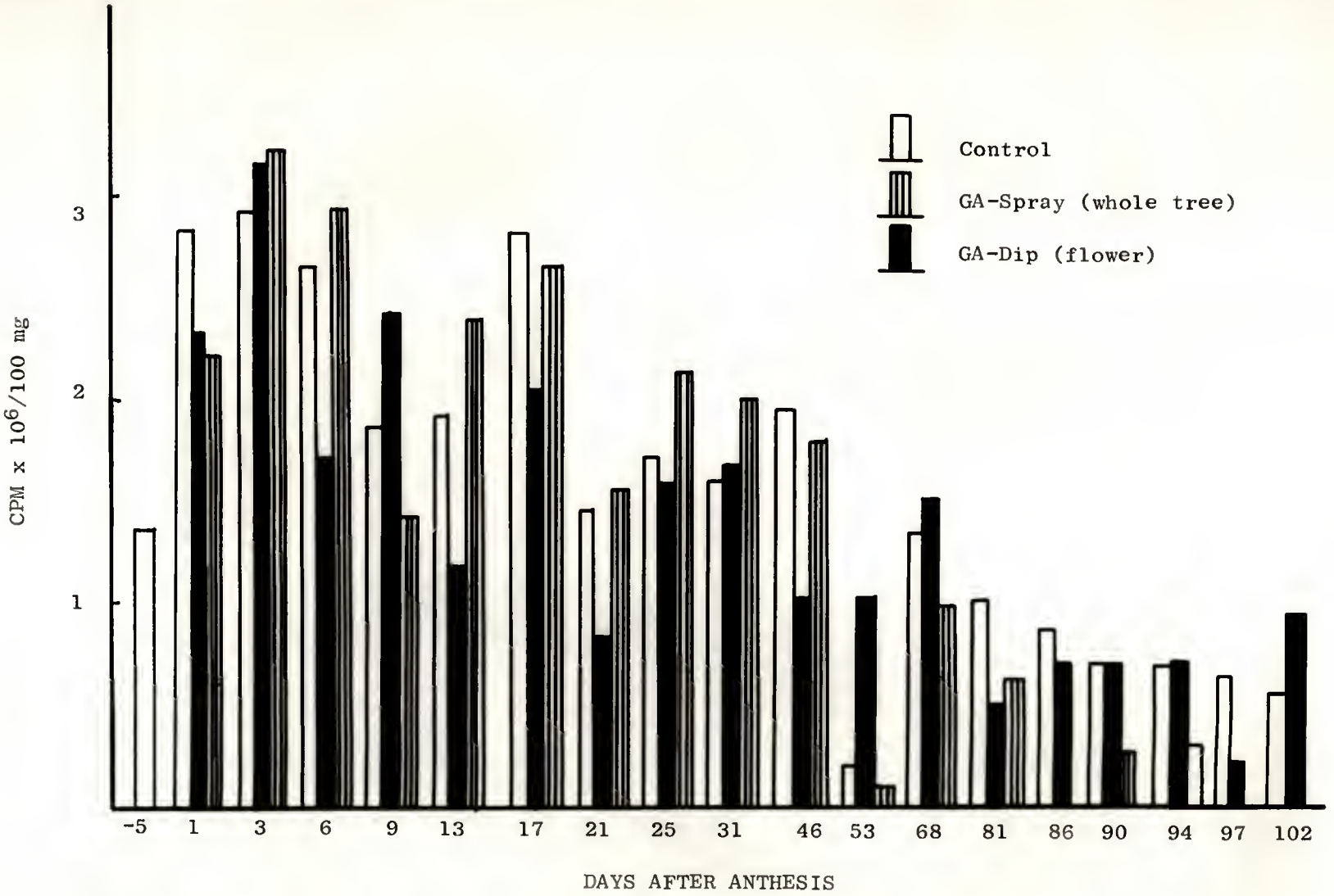

Fig. 16. Comparisons of ^{14}C retained in a median leaf after a 4-hr exposure to $^{14}CO_2$ during fruit set as influenced by GA treatments.

There did not appear to be any substantial differences due to treatments; however, leaves of the sprayed trees retained more of the labelled photosynthate during the first 46 days than the others and the GA-dip treatment retained less, which agrees with the patterns of export to the fruit from the same source leaves.

Retention of ^{14}C in the previous - flush source leaves followed a bell-shaped curve, which peaked during the period of maximum import into the fruit from the new-flush source leaves (Fig. 17).

There appeared to be greater retention of labelled material in the previous - flush source leaves from the GA-spray treatment during the beginning of the experiment, but little difference was observed after the 1st 25 days.

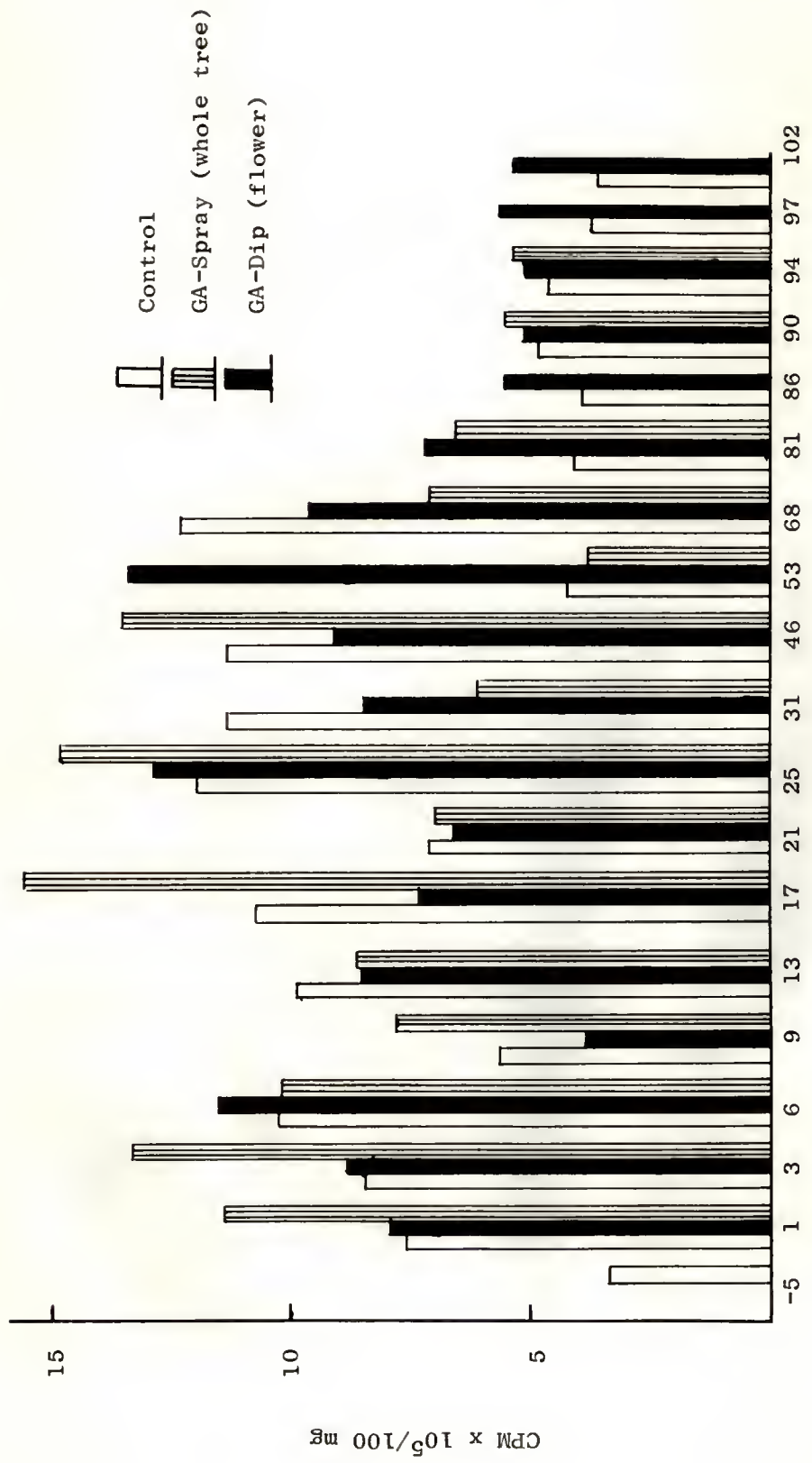

Fig. 17. Comparisons of ^{14}C retained during fruit set in a leaf of a previous flush subtending a new shoot after a 4-hr exposure to $^{14}CO_2$ as influenced by GA treatments.

DISCUSSION

Conditions desired for this study were established: i.e., an increase in fruit set with flowers dipped in GA, no increase in fruit set from whole-tree sprays and low fruit set on control trees. Fruit counts were not taken but it was evident from the number of tagged fruit remaining on each treatment at the end of the experiment that the fruit set on the GA-dip treatment was much greater than the GA-spray treatment or the control. The GA-spray treatment did not cause any increase in fruit set. These results confirm previous research in Florida. In this study, trees treated with whole-tree sprays shed some of their leaves whereas no loss of leaves was observed in previous studies on navel orange when concentrations up to 500 ppm GA were used (53). On the other hand, GA applied to navel oranges in California has resulted in leaf drop and twig dieback even at concentrations below 250 ppm (41). Such differences in response have not been explained, but differences in climate or specific weather conditions at the time of spraying may contribute to the response by affecting absorption or the amount of material deposited on the leaf.

More ^{14}C-metabolites moved into the ovaries and young fruit throughout the fruit-setting period from both current season and previous season leaves following GA-dip treatment than was found with untreated trees or those sprayed with GA. In addition, there was a short period from 6 days to 13 days after anthesis, in which fruit that had been dipped in GA received much more ^{14}C-photosynthates than fruit from the GA-spray treatment or the control.

The period immediately following anthesis appeared to be a critical time in fruit set. It was a transitional time in which the primary source of photosynthates received by fruit shifted from the old leaves to the current flush. Newly developing leaves and fruit initially imported photosynthates from mature leaves subtending the new flush. New leaves gradually ceased to import as they matured and they began to export photosynthates to the developing fruit when they were fully expanded. The older mature leaves gradually became a less significant source of photosynthates for the fruit. Fruits which had been dipped in GA received a substantial supply of photosynthates without interruption; whereas fruit from the GA spray treatment and the control had a period of approximately 7 days in which the total amount received from both mature leaves and new leaves was quite low. This time coincides with a normal wave of heavy fruit drop. There was a heavy fruit drop from the control of this experiment during that period, but with the GA-spray treatment, the other weak fruit-setting treatment, fruit drop was lighter. However, fruit from the GA-spray dropped later in the experiment. Abscission was delayed, but there was not a strong movement of photosynthates into fruit from surrounding leaves and the small fruit gradually dropped as evidenced by very few fruit remaining on trees sprayed with GA at the termination of the experiment.

These data could explain greater fruit set in the GA-dip treatment because they follow the hypothesis of Crane (22) that growth regulators promote fruit set by establishing a high rate of metabolic activity in the ovary resulting in a continuous flow of metabolites from other parts of the plant into the fruit. Cytokinins applied to newly developing navel

oranges have been demonstrated to enhance importation of ^{14}C-labelled photosynthates from nearby leaves (49). Furthermore, fruit from 'Calamondin' flowers which had been emasculated and then treated with GA, received a continuous flow of ^{14}C-labelled photosynthates from nearby leaves as was also the case with seedy fruit of the same cultivar, but not when flowers were emasculated (85).

This does not, however, explain why there was a stronger movement into ovaries and young fruit of the flower dip treatment than when entire trees were sprayed with the same concentration of GA. One might speculate that the leaves become more competitive than the fruit for substrates due to the spray application of GA on the leaves; however dry wt data of the leaves do not substantiate this hypothesis. GA in the leaves may have, however, caused a higher rate of respiration, creating a higher demand for substrates but not causing the accumulation of more dry material than non-sprayed leaves. Data showing translocation of ^{14}C-photosynthates from old leaves into new leaves subtending the fruit support this hypothesis. There was more photosynthate moving from the old leaves into the new leaves in the GA-spray treatment than in the GA-dip treatment or the control during the period following anthesis, which appears to be a critical time in fruit set. This time coincides with the period in which translocation of current photosynthates to fruit of the GA-dip treatment was greater than the movement of photosynthates to the GA-spray treatment or the control. Therefore, the GA-spray may have caused an increase in demand for substrates by the new leaves making them more competitive for substrates than fruit of that treatment while fruit that had been dipped in GA became more competitive than the leaves of the treatment which

had not received any GA. This hypothesis could be clarified by an experiment designed to determine the respiration rate of navel orange leaves in which these treatments had been imposed.

Another possibility is that spraying an entire tree may have created a multitude of sites in which metabolic gradients were established, but none had a particular competitive advantage so that the total effect was similar to the control. Translocation patterns in fruiting shoots of the GA-spray treatment and the control were very similar throughout the experiment which would support this premise. In addition, the fruit wt data demonstrate that the control fruits remaining on the tree at the end of the fruit-setting period were just as large as fruits from the GA-dip treatment, whereas fruits from the GA-spray treatment were much smaller. One might assume that the control fruits that set did so because their ability to compete for substrates was greater than those that did not set. The few fruits that did survive were apparently as competitive for substrates as fruit that had been dipped in GA. If the premise that a multitude of sites are activated by spraying the tree with GA be true, then the competitive advantage of the few fruits on the tree that would have set without treatment becomes diluted by the many competing sites and the resulting fruits would be smaller, which was the case in this experiment. This premise might be determined by dipping varying quantities of flowers on a tree with GA, including 1 treatment in which all flowers on the tree would be dipped in GA. Another means would be to compare translocation patterns of the treatments imposed on this experiment in a cultivar, such as 'Orlando', in which fruit-set is increased by GA-sprays to the translocation patterns of the same treatments on

navel orange. Crane's hypothesis should then be re-evaluated if the translocation patterns in the GA-spray treatment of 'Orlando' did not differ from the control, as in this experiment.

There is a chance that flowers are not sufficiently wet by spraying navel trees with GA. This could be determined by spraying an entire tree with GA then dipping selected flowers in the same concentration of GA and tagging other flowers without dipping to determine if there would be a difference in fruit set due to treatment.

Many questions relating to the cause of failure of GA sprays to improve fruit set of navel oranges remain unanswered; however, it is clear from this study that there was a much stronger flow of metabolites into fruit from the GA dip treatment, the most effective fruit setting treatment, than into fruit of the other treatments. There appears to be a critical time in fruit set, following anthesis, in which the principal source of substrates switches from older leaves to the new leaves subtending the fruit. These data suggest that a smooth transition must take place causing no interruption in the flow of substrates to the fruit for fruit set to take place.

SUMMARY AND CONCLUSIONS

1. Large increases in yields have occurred when either navel orange flowers or fruit were dipped into solutions of gibberellic acid, but GA has been ineffective when sprayed on entire trees. The role of growth regulators appears to be related to the supply of leaf-metabolites to the young fruit, hence this work was to investigate the movement of leaf metabolites in the 'Washington' navel orange following application of GA both as flower dips and as whole-tree sprays.

2. More fruit remained at the conclusion of the fruit-setting period, through the June crop, on the GA-dip plots than on the GA-spray or control plots.

3. Movement of ^{14}C-photosynthate into fruits from the GA-dip treatment was greater than the GA-spray treatment or the control.

4. There was a stronger movement of ^{14}C-metabolites into the ovaries and young fruits throughout the fruit-setting period from both current season and previous season leaves of the GA-dip treatment than for untreated trees or those sprayed with GA. In addition, the GA-spray treatment and the control had a period of reduced transport from old leaves to fruits, following anthesis, before new leaves began exporting significant quantities to fruits.

5. Dry wt of fruits from the GA-dip treatment and the control was much greater than fruit from the GA-spray treatment.

6. There was bidirectional movement of labelled photosynthate from the median leaf on the shoot; however, the greatest quantities were transported acropetally, fruits being the primary site of importation.

7. The strongest fruit-setting treatment maintained a greater movement of metabolites from the leaves into fruits than other treatments, substantiating the hypothesis that growth regulators promote fruit set by enhancing the movement of metabolites into fruits. The failure of whole-tree sprays of GA to enhance fruit set of navel orange appears to be due to an inability of the fruit to attract metabolites in sufficient quantities to maintain fruit growth during the fruit setting period.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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